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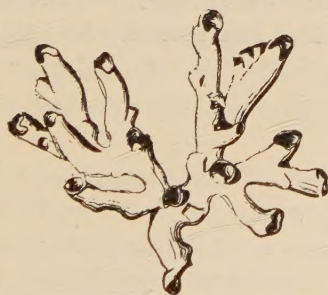


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BLASTOGENY AND INDIVIDUAL VARIATIONS IN TETRACORAL  
COLONIES FROM THE DEVONIAN OF POLAND

**Abstract.** — In order to investigate the process of blastogeny and individual variations in tetracoral colonies, comparative studies have been made of the following forms from the Middle and Upper Devonian strata of Poland: *Disphyllum geinitzi* L. & S., *Hexagonaria laxa* Gürich, *Hexagonaria laxa jurkowicensis* n. subsp., *Peneckiella minor kunthi* (Dames) and *Sudetia lateseptata* n. gen., n. sp.

INTRODUCTION

A stimulus to the study of individual variation in colonies of a given tetracoral species has been provided to the writer by Professor R. Kozłowski, Head of the Palaeozoological Institute of the Polish Academy of Sciences. The most sincere words of gratitude are here conveyed to him for this suggestion as well as for his constructive criticism and revision of the manuscript.

Thanks are due to Mrs M. Pajchel and Dr J. Czermiński for important information on Devonian deposits of the eastern part of the Holy Cross Mountains (Góry Świętokrzyskie) and for the courtesy of discussing with the writer the associated stratigraphic problems.

Acknowledgement is similarly made to Mrs J. Gruszczyńska for the execution of graphs and drawings from photographs of thin sections, and to Mrs J. Humnicka for the English translation of the Polish text.

The writer's one month visit at the Palaeontological Institute of the Polish Academy of Sciences of the U.S.S.R. in Moscow was sponsored by the Polish Academy of Sciences. The deepest thanks are expressed to Professor A. Orlov, Director of the Institute, for the untiring courtesy and the free access to the greatly valuable Devonian tetracoral collections which have been worked out by Dr E. D. Soshkina, a leader of the study of this group.

T. A. Dobroljubova, an authority on Carboniferous corals in the Soviet Union, has given the writer access to her collections and held some most interesting discussions on Carboniferous colonial tetracorals and their



variability. Sincere thanks are here conveyed for the friendly assistance tendered by her during the writer's visit in Moscow.

Similar acknowledgements are made to: N. V. Kabakovitsh of the Academy of Sciences in Moscow, V. A. Sytova of the Lomonosov Moscow University, and Dr V. A. Ivania of the Tomsk University.

Professor A. v. Schouppé of the Münster University in Westphalia, has been kind enough to exchange critical remarks on Devonian corals. The writer is obligated to him for sending some greatly useful microscopic sections of the topotypes of *Peneckiella minor* (Roemer) from Grund.

Sincere thanks are likewise due to Professor H. Flügel of the Graz University, for his letters containing most interesting remarks and for sending tetracoral specimens from the Devonian of Austria.

\*

In the text and explanations of tables and figures the following abbreviations are used: *c1-c9* — successive classes, *Mn* — arithmetic mean of septa in classes, *Mn I* — arithmetic mean of major septa, *Mn II* — arithmetic mean of minor septa, *Md* — arithmetic mean of calyx diameters, *Mc* — correlation coefficient of classes, *Ms* — correlation coefficient for species, *Mt* — mean diameter of tabularium.

#### PALAEOECOLOGICAL CHARACTERISTICS OF LOCALITIES

*Disphyllum geinitzi* Lang & Smith occurs at Sitkówka (S of Kielce) in large phaceloid colonies. A part of a colony, approx. 0.5 m long, has been recovered there, probably from its natural biotope. The rock embedding the colony is a grey zoogenetic limestone of Upper Givetian age. The Givetian here is embraced by the Gałęzice syncline (fig. 1). It crops out in a big quarry near to the local railway station. According to Gogolczyk (1956, 1959), the occurrence is here noted of banks with *Amphipora ramosa* (Phillips) and *Stachyodes caespitosa* Lecompte, and — according to Stasińska (1958) — that of *Thamnopora cervicornis* (de Blainville). Fragmentary isolated tetracorals, e.g. *Thamnophyllum trigeminum* Pen. and some thick-walled *Disphyllum geinitzi* are sporadically encountered. The exposed surface of the above mentioned *D. geinitzi* colony has been strongly weathered so that the corallite walls are mostly strongly damaged. Hence, thin sections have been cut mainly in the deeper portion of the colony. On one side the surface of the colony is covered by numerous shells of *Atrypa* sp. from the *aspera* group. The rock cementing the corallites consists of fragmentary specimens of *D. geinitzi*, remains of *Atrypa* sp. and fragments of other organisms occurring in the vicinity. Thus it is probable that the colony was formed in situ.

The fragility of the colonial skeleton, its fasciculate pattern, the parallel upwards growth of corallites, showing no conspicuous divergence, also the



Fig. 1. — Sketch map showing distribution of localities

tail skeletons of the surrounding fauna, all suggest that the biotope of this coral bank was a calm sea or quiet lagoon (Kühn, 1926, p. 130).

*Hexagonaria laxa* Gürich was found in a stromatoporoid-tabulate reef at Dziewki, 4 km north of the township of Siewierz. Gürich (1896, p. 73), when describing the coral limestones of Dziewki, mentions *H. laxa* among the long list of fossils there.

Śliwiński (1956) ascertained that Givetian limestones at Dziewki stretch out in a belt 2250 m long and 250 m wide. Reef limestones occur at the western end, dipping NE at an angle of  $25^\circ$ . The predominance of *Amphipora* banks is noted in the western portion, that of globose stromatoporoids in the east and south. Intercalations packed with colonial *Hexagonaria laxa* occur in the north-eastern walls near to the pond. Next to them are noted layers with *Plagiopora dziwkiensis* Gürich, *Striatopora costata* Blum. and beds of *Stachyodes verticillata* (M'Coy). In Mr Śliwiński's opinion, the presence of *Stringocephalus* suggests the Givetian. The



presence of corallites from the tetracoral family of Stringophyllidae, including the genera *Stringophyllum* sp. and *Neospongophyllum* sp. (the latter approaching *Sinospongophyllum planotabulatum* Yoh; Yoh, 1937, p. 56, 57), is suggestive of the upper Middle Givetian (after Wedekind's stratigraphic chart of 1924).

Since *Hexagonaria* colonies recovered from the bed are usually small and strongly weathered, that selected by the writer as topotype for the study of variations was 30 cm long and embedded in a huge limestone boulder. The same rock contains an abundant fauna of above mentioned fossils. It is a reef limestone, probably formed at the lagoon side, as is indicated by the frail skeletal structure of the colony and the predominance of ramose forms in the associated fauna. *H. laxa* populations have persisted in their natural biotope within the stromatoporoid-tabulate reef.

*Hexagonaria laxa jurkowicensis* n. subsp. — A stromatoporoid-tabulate reef, locally crowded with globose stromatoporoids of the genera *Actinostroma* and *Stromatopora*, is under exploitation in a quarry adjacent to the Jurkowice wood, about 4 km west of Opatów (Samsonowicz, 1917, p. 39). A mass occurrence is likewise noted there of circular colonies of *Alveolites suborbicularis*, *H. laxa jurkowicensis*, individual tetracorals, also *Amphipora* beds and large brachiopods. The complete reef population here occurs in situ. Large circular colonies of Stromatoporoidea, Tabulata, also the globose *Hexagonaria* with thick skeletal structure, suggest a reef exposed to the strong action of waves (Kühn, 1926, p. 130). According to Samsonowicz (1917), reef limestones are encountered in the Żerniki-Karwów syncline, stretching from the Pokrzywianka (Żerniki) to the Łagówka (Karwów). They share in the composition of Givetian and Frasnian rocks of this syncline.

*Peneckiella minor* (Roemer) *kunthi* (Dames) and *Sudetia lateseptata* n. gen., n. sp. — These two species are reef-builders at Mokrzeszów<sup>1</sup> in the Sudeten Mountains. The Mokrzeszów rocks participate in the composition of the Świebodzice basin lying in the north-western corner of the gneiss Sowie Mountains block. This is a deep Hercynian synclinalorium filled in by non-metamorphic Upper Devonian and lowermost Culm rocks (Reg. Geol. Polski, 1957, p. 93-100). Marine transgression here began during the *Manticoceras* period. The sea was on the whole a shallow one and flooded basins cut off by barriers. The Świebodzice Devonian displays diversity of character with rapidly altering facies: conglomerates, greywackes, shales, limestones and marls. Limestone intercalations are usually rather small, the only larger one being that of Mokrzeszów; it is 200 m in length, exploited to its very limits and now under Nature Protection. It crops out

<sup>1</sup> Oberkunzendorf — of the German authors.



round an overflowed abandoned quarry, being part of the coral reef running NW from Witoszów across Mokrzyszów. The occurrence of land south of this reef seems very probable.

Mokrzyszów has been made known by descriptions of the fossils recovered there. In 1873, Dybowski (pp. 402) described two coral species from that reef: *Spongophyllum pseudovermiculare* M'Coy (= *Tabulophyllum priscum* (Münster)) and *Fascicularia kunthi* (Dames) (= *Peneckiella minor kunthi*). In 1939, Pawlik worked out the stratigraphy of the Upper Devonian of Świebodzice, Mokrzyszów included. The following beds have been here differentiated by that author: 1) top conglomerates; 2) Famennian clay shales with *Cheiloceras sacculum* Sandb. etc.; 3) marly brachiopod limestones and shales with numerous globose algae *Sphaerocodium zim-mermanni* Rothpl., including *Productella sericea* Dames, *Spirifer archiaci* Furch. and *Productus hallanus* Walcott; 4) limestones crowded with coral fossils. They comprise a reef built up by *Peneckiella minor kunthi* and *Sudetia lateseptata*. There are also banks with *Tabulophyllum priscum* and Tabulata of the genera *Thamnopora*, *Coenites* and *Alveolites*.

Tetracorals are the main builders of the Mokrzyszów reef. Stromatoproids are completely lacking. According to Lecompte (1954), Palaeozoic reef corals were considerably less susceptible to the presence of clay suspensions than their contemporaneous Stromatoporoidea and the living Hexacoralla. Therefore, they were able to exist in somewhat deeper waters, while stromatoporoids lived within the surf zone (l. c., p. 171). It may thus be inferred that the Mokrzyszów reef either developed in somewhat deeper waters than did the reef-building stromatoporoids, or that the pelitic suspensions driven from the nearby land were not harmful to the coral reefs with *Peneckiella minor kunthi* and *Sudetia lateseptata* though they were unfavourable to the development of massive stromatoporoids.

## DESCRIPTIONS

### *Disphyllum geinitzi* Lang & Smith, 1935

(fig. 2-8)

35. *Disphyllum geinitzi* L. & S.; W. D. Lang & S. Smith, *Cyathophyllum*..., p. 570, 571, fig. 26; pl. 36, fig. 1-3.

**Material.** — A large phaceloid colony 17×12×30 cm, recovered from co-genetic limestones in the southern wall of the Kostrzewa quarry at Mokrzyszów (fig. 1). 34 thin slides with transverse and longitudinal sections.

**Diagnosis.** — Subcylindrical corallites forming phaceloid colonies, usually with coalescing walls, or calicinal expansions. Corallites circular in

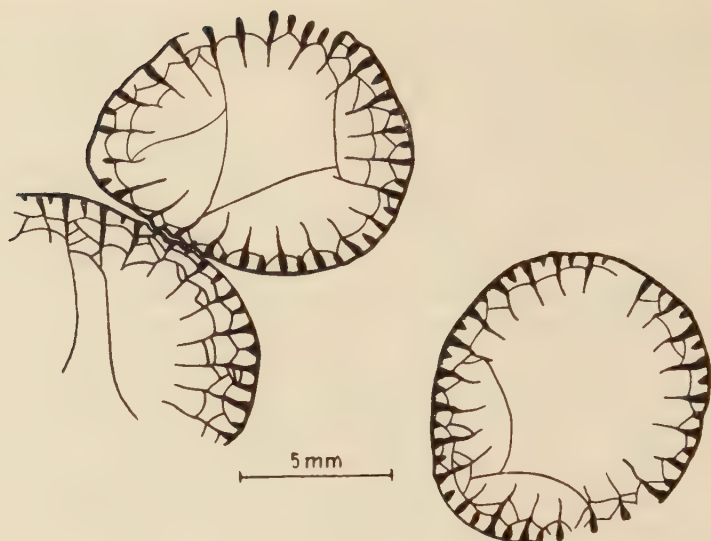


Fig. 2. — *Disphyllum geinitzi* Lang & Smith; Sitkówka, Givetian. Cross section of corallites (slide no 2).

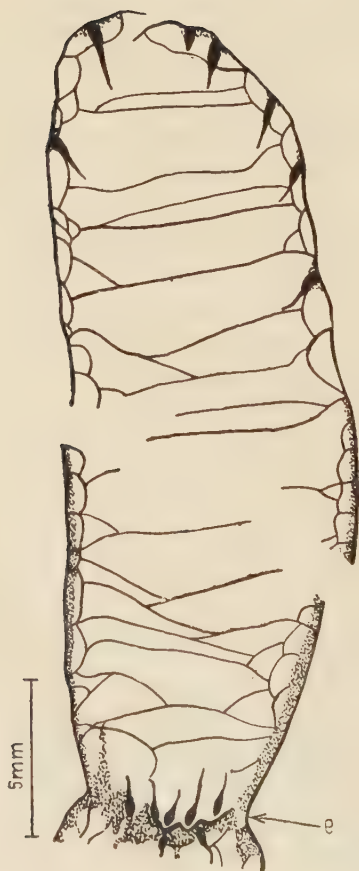


Fig. 3. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Longitudinal section of mature individual separated from bud by partly formed new epitheca — e (slide no 1).

section (fig. 2), mature individuals 9.5 to 11.5 mm in diameter, 22—24 major septa with length one-fourth that of the calyx diameter, minor septa extremely short: one-fourth to one-fifth the length of major septa. Beneath the epitheca<sup>2</sup> is the outer pseudotheca, and near it — the inner pseudotheca. One row of minute dissepiments; tabularium broad, consisting of generally complete tabulae either flat or slightly arched. Budding<sup>3</sup> lateral, trabecular microstructure of the disphylloidal type.

Footnotes 2 and 3 — see opposite page.

### A. Blastogeny

1. *Development of bud* (fig. 4-8). Buds are produced in the periphery of the calyx. Within the studied colony budding is not frequent. Even young corallites are rare too. The following stages may be distinguished in the budding process.

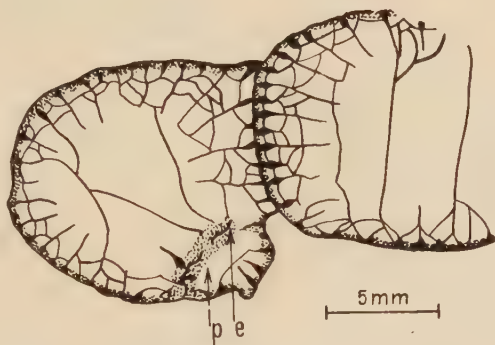


Fig. 4. — *Disphyllum geinitzi* L. & S.; Sitkóvka, Givetian. Cross section of a bud in nepionic stage; rudimentary new epitheca (e) and pseudotheca (p), (slide no 6).

a) Stage I (fig. 4) — the budding corallite doming outwards. The wall separating the bud from the parent corallite begins to be laid down and, on either side of it, new irregular zigzag septa are produced, on one side belonging to the bud, on the other — to the budding corallite. Septa present

<sup>2</sup> In view of the confused meaning of the term "wall" the writer thinks it necessary to state that in her present paper she distinguishes the epitheca (which is the outer mantle of the corallite) from the adjacent wall. The wall is the pseudotheca since it consists either of thickened distal ends of septa (septothecca) connected by a laminate stereozone, or of thick-walled dissepiments (parathecca). The epitheca is a thin layer of stereozone deposited on the wall (on the outer pseudotheca). In the past were considered representatives of Disphyllidae and Thamnophyllidae the occurrence of the pseudotheca exclusively and of septothecca and parathecca. In cerioid colonies of Disphyllidae, each corallite is surrounded by the outer pseudotheca and the epitheca. In cerioid Thamnophyllidae the outer pseudotheca only is present, while in the phroidal (e. g. *Phillipsastraea ibergensis progressa* Rozk.) the individual polyps are not isolated from each other by a wall. Hence Alloiteau (1955, p. 424) is not correct in postulating the presence of at least a thin wall in colonial tetracorals. An inner wall often occurs next to the outer. It is the pseudotheca made up of septa and dissepiments which are here locally thickened by the deposition of stereozone.

<sup>3</sup> Every one of the examined blastogenies is originally intracalicular, subsequently the bud becomes lateral if it bends outwards at a certain angle from the parent corallite: the bud is intermural if it develops between the walls in the cerioid corallum, parricidal — if it occupies the whole inside, while the parent corallite dies.



before the beginning of budding occur along the outer bud wall. The wall separating the bud from the parent corallite is not yet completed; it consists of three layers: the epitheca which is in common, and two pseudothecae. These belong on one side to the bud, on the other — to the budding corallite. Such a triple wall is always formed during the blastogeny in *Disphyllum*, hence this type of budding may be called "disphylloidal".

b) Stage II (fig. 5) — the bud has nearly completely separated from the parent corallite, it is 4.5 to 4.7 mm in diameter, the number of septa

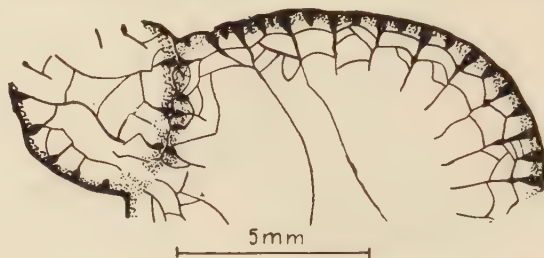


Fig. 5. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Cross section of a bud in late nepionic stage; partly formed epitheca and new septa (slide no. 3).

is 18, some of the septa are shorter. One bud only is generally produced; if there are two — they may or may not be of the same age (fig. 6), separated from the parent corallite and from each other by the characteristic triple wall. Fig. 7 represents a budding corallite in longitudinal section. The lateral bud bends outwards at an angle of  $75^\circ$ , growing out from the dissepimental area of the mature corallite. During the nepionic stage the wall separating the bud has not yet been completed, the periaxial part of the budding corallite tabula is the first tabula of the bud. The bud is still in close depen-

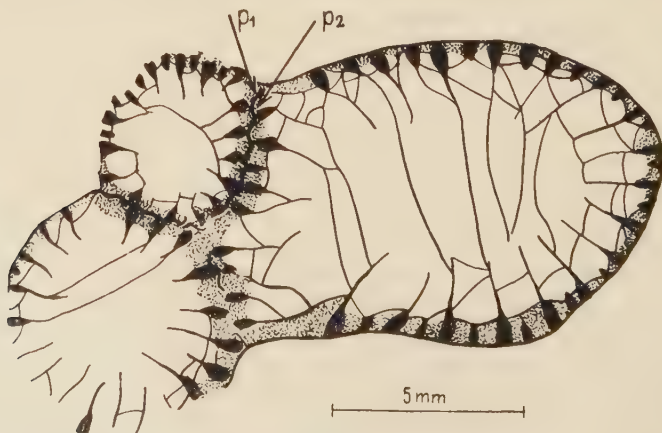


Fig. 6. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Cross section of a bud in early neanic stage; new epitheca nearly complete between two pseudothecae ( $p_1$ ,  $p_2$ ) in three corallites intimately fused by budding (slide no. 5).

hence on the parent corallite. The neanic stage begins slightly higher up; it is indicated by the appearance of the "triple" wall. Along this wall the bud as well as the parent corallite display diaphragmatophoric structure.

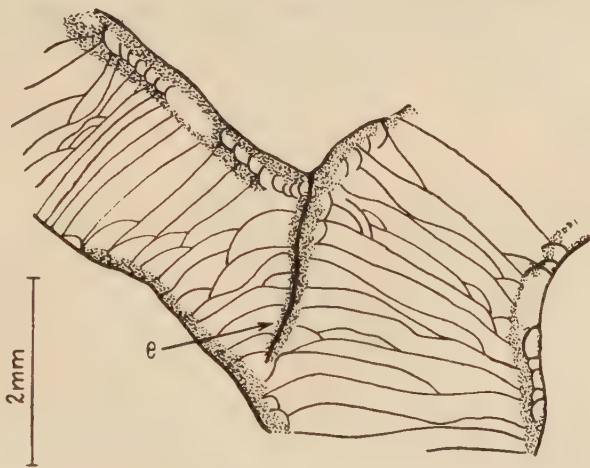


Fig. 7. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. Longitudinal section of a bud with epitheca (e) separating it from parent corallite in the neanic stage (slide no. 7).

Dissepiments appear directly before the bud has bent outwards from the budding individual. The structure becomes pleonophoric. The juvenile corallite is at that time 5 mm in diameter.

2. *The n/d ratio variations during ontogeny.* There is close correlation between the number of septa (n) and the diameter of calyx (d). In the ephebic stage corallites produce buds even when only 7.2—8.5 mm in diameter and with 20—22 major septa. Table 1 shows the mean number of septa at mean diameter of calyx in each of the mentioned classes.

Table 1

Mean number of septa (Mn) at mean diameter of calyx (Md) ratio with respective coefficients (Mc, Ms)

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9
Mn I	12	14	17.5	19	20.3	22.5	23	24	24
Md	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5
Mc1-Mc9	3.4	3.1	3.1	2.9	2.7	2.6	2.4	2.3	2.1

Ms  $n/d = 2.75$

The above data indicate less rapid increase in the number of septa in the diameter of calyx. This is negative allometry in relation to

septa. The value of the  $n/d$  ratio decreases slowly in the progressively higher classes. The number of septa (24) in the two highest classes becomes static.

The  $n/d$  ratio curve (fig. 8) rises considerably in the juvenile stage, deviating nearly uniformly from either axis. In individuals with 22 or more

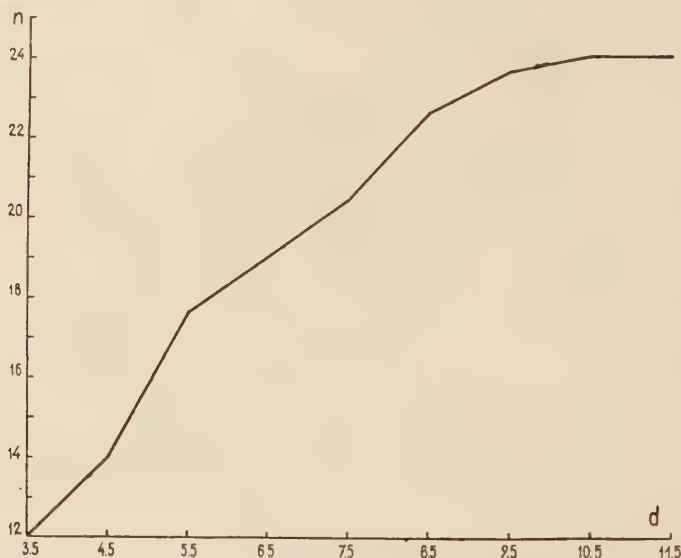


Fig. 8. — *Disphyllum geinitzi* L. & S.; Sitkówka, Givetian. The  $n/d$  ratio curve; corallite diameters ( $d$ ) — on abscissa, number of major septa ( $n$ ) — on ordinate.

septa this curve is subparallel to the X axis, since increase of diameter distinctly dominates over increase in number of septa. In character the  $n/d$  ratio curve approaches that of the  $n/t$  ratio in *Hexagonaria laxa* (fig. 15), since they display similar dynamics during ontogeny.

### B. Individual variations

Individual variation within the colony is not strong. Corallites are in obvious harmony with environmental conditions. They have attained their optimum development and this is emphasized by their complete adaptation. The corallite structure is not complex. The skeletal elements are fully developed and do not bear signs of regression. When any slight variations do occur, they are phenotypic, seemingly expressing direct reaction to the position occupied in the colony and to the danger of being covered up with sediments, which threatens the corallites.

1. *Colonial variability pattern.* Practically throughout its length the colony is phaceloid, some less crowded places occur, however, where buds bend out at a slightly greater angle. There the appearance of the colony becomes dendroid.



2. *Tabularium(t)/dissepimentarium(diss) ratio*. At diameter of 5 mm the t/diss ratio is 3.7:1.3. Thereafter the tabularium width increases reluctantly, while the dissepimentarium augments but little. In somewhat larger corallites the t/diss ratio is as follows (in mm):

$$9.0 : 1.9 = 5.0$$

$$9.0 : 1.2 = 7.5$$

$$9.5 : 1.8 = 5.0$$

$$9.5 : 1.5 = 6.3$$

$$10.0 : 1.2 = 8.3$$

These data show lack of uniformity in dissepimentarium width variations. There is no correlation between the tabularium and the dissepimentarium. Another row of vesicles or a larger dissepimentum makes its appearance in reaction to incidental stimulus, and thus the t/diss ratio is diminished.

3. *Number of tabulae in 2 mm*. The arrangement of tabulae varies strongly even within one individual. Their spacing is controlled by outside factors only and it is not coordinated with any structural characters. E. g. at diameter of 8.5 mm the number of tabulae over 2 mm ranges from 2 to 8.

4. *Basal thickness of septa*. During the juvenile stage septa may be thick and hence laterally coalescent, so as locally to form a continuous stereozone. In some corallites the walls are thickened even during the ephebic stage. In our colony the septa are mostly slender and widely spaced even during early ontogeny. Both the major and minor septa are with the same basal thickness. About 80 septa have been measured in corallite sections from one colony, providing the following data:

Thickness (in mm)	Per cent of septa
0.1	3
0.2	20
0.3	40
0.4	30
0.5	7

5. *Length ratio of major and minor septa*. Both types of septa are short, but the length of major septa is several times that of minor, as is shown here below:

Per cent of major septa	X-times as long as minor septa
10	three
40	four
30	five
20	seven to nine

The length of major septa and their length ratio to minor septa depends mainly on the site of the section. In one cut in between the tabulae the major septa are short, while in another cut across the tabula they are longer, so much so as to be nine times the length of minor septa.

*Hexagonaria laxa* Gürich, 1896

(fig. 9-16)

1896. *Hexagonaria laxa* Gürich; G. Gürich, Das Palaeozoicum..., p. 172-173, pl. 4, fig. 5.

*Material.* — One large colony from the zoogenetic limestone of Góra Kadzina, north of the Dziewki village. Also 30 detached colonies from the eastern quarry wall. 25 thin slides prepared from the large colony, including cross and longitudinal sections.

*Diagnosis.* — Colonies tabular, cerioid (fig. 9). Calices separated by thin epitheca, deep, with steep flanks and flat bottom. Maximum diameter  $12 \times 12$  mm, tabularium 5.5 mm, greatest number of major and minor septa 38. Septa amplexoid, with tendency to split up into radial rows of



Fig. 9. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a cerioid colony (slide no. 8).



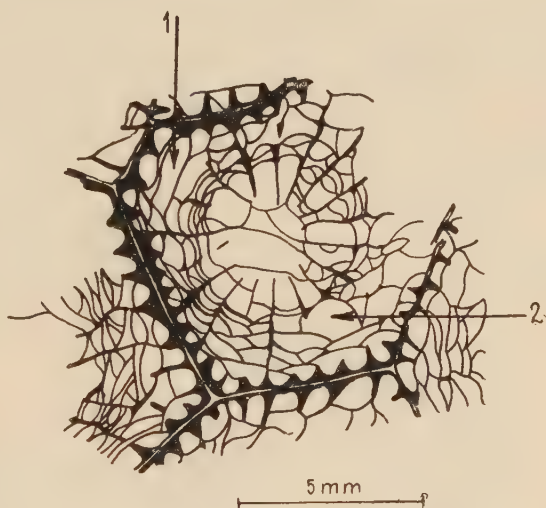
Fig. 10. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Longitudinal section of a cerioid colony (slide no. 10).

spines, provided with carinae. Dissepimentarium broad; distinct inner pseudotheca between tabularium and dissepimentarium; tabulae horizontal or slightly arched, complete or incomplete, with supplementary plates (fig. 10). Budding intermural. Microstructure trabecular of the disphylloid type.

## Blastogeny

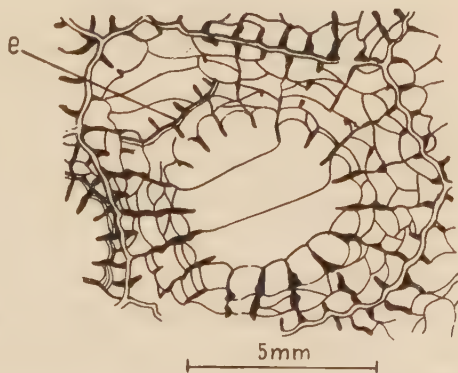
1. *Development of bud.* The corallite attains maturity with greater diameter (8—10 mm) and 36—38 septa present. Buds are produced in place of the maximum width of the dissepimentarium, dissepiments notably large. In this part of dissepimentarium major septa have been reduced to

Fig. 11. — *Hexagonaria laxa*  
Mürich; Dziewki, Givetian.  
Cross section of a corallite  
taking place for two buds —  
1, 2 (slide no. 11).



short conical bases in the periphery, a row of spines on dissepiments and a larger spine on the inner pseudotheca. Several ontogenetic stages are observable in cross section of the bud.

Fig. 12. — *Hexagonaria laxa*  
Mürich; Dziewki, Givetian.  
Cross section of a bud in ne-  
pionic stage; e new epitheca  
of bud (slide no. 8).



a) In stage I — space is prepared for the new bud (fig. 11). Bases of septa only are discernible in the periphery. Septa of dual length here very even. Nearer to the axis dissepiments only are seen. Among them, two or three vesicles slightly larger than others have the walls united



into an arch concave towards the corner, and forming the initial wall of the new bud. This is the new epitheca separating the budding corallite from the parent.

b) In stage II (fig. 12) — the new wall of the bud has thickened since new septa have been produced. Their dilated ends are attached to the epitheca. Major septa of the parent corallite are attached to the other surface of the epitheca, with minor septa soon arising between them. A new outer pseudotheca is thus formed on this side of the epitheca too. The wall separating the bud from the parent corallite is "triple", similarly as in *D. geinitzi*. The new bud wall is very close to the inner pseudotheca of the parent corallite. Hence it is clearly seen by which of the adjacent corallites the bud has been produced.

c) In stage III (fig. 13) — the new bud wall is not yet complete. One of its ends leans against the outer wall of the parent corallite, the other against a major septum. Eight short septa have arisen on the new wall.

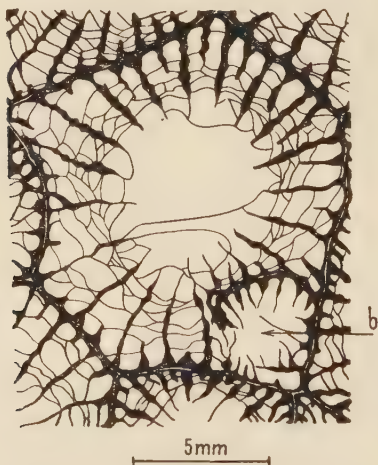


Fig. 13. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a bud (b) in late nepionic stage; epitheca still incomplete (slide no. 12).



Fig. 14. — *Hexagonaria laxa* Gürich; Dziewki, Givetian. Cross section of a bud in neanic stage (slide no. 13).

d) In stage IV, neanic (fig. 14) — the bud is wholly surrounded by the epitheca. Septa have united into one thick wall. From it protrude the axial ends of major septa (18), nearly reaching to the axis, also minor septa have appeared not protruding beyond the wall. Major and minor septa of the parent corallite, as well as its dissepiments, are still discernible in one corner.

e) In stage V (ephebic) — the number of septa does not increase, but the calyx is widened; septa grow longer, slender and more widely spaced;

major septa differ distinctly from the minor in their length. Septa are panned by vesicles, and carinae appear on the septa. There may be as many as 38 septa. Buds are produced in corners when space for them is available.

Fig. 10 shows the ontogeny of the bud in longitudinal section. The vesicles form a base for the bud, while the next dissepiment is the first tabula. One wall is made of the thick-walled, periaxial dissepiments of the parent corallite, the other of the outer corallite wall. In early youth this is the diaphragmatophoric stage. Somewhere higher up, with diameter of 1 mm, commences the pleonophoric structure, when dissepiments appear on one side.

The budding process in *Hexagonaria laxa* resembles that in the phaeoloid form *Disphyllum geinitzi*.

2. *The n/t ratio variations during ontogeny.* Observations and graphs show close correlation of these two characters. The value of the n/t ratio decreases progressively during ontogeny, as is shown in table 2.

Table 2

Mean number of septa (Mn) and mean diameter of tabularium (Mt) ratio with respective coefficients (Mc, Ms)

Classes	c1	c2	c3	c4	c5	c6	c7
Mn I, II	24	31	32	35	36	37	38
Mt	2.8	3.3	3.8	4.3	4.8	5.3	5.8
Mc1-Mc7	8.6	9.4	8.4	8.1	7.5	7.0	6.5

Ms n/t = 7.9

During youth the number of septa increases rapidly from 24 to 35. The class correlation coefficient augments slightly in class 2. Later its value diminishes since the number of septa has slightly augmented, while the tabularium diameter continues uniformly to increase.

These developmental dynamics are excellently illustrated by the n/t ratio graph in fig. 15. In the nepionic stage the number of septa increases rapidly. In the next, neanic stage the rate of increase is cut down. In mature corallites, with 35—38 septa, the increase is extremely slow.

Budding is not frequent in the studied colony. Among the 17 thin slides prepared from 99 corallites in transverse section, three only budding specimens have been discovered by the writer. Most probably budding on

a mass scale occurs at the beginning of colonial growth, while later corallite bundles grow straight up.

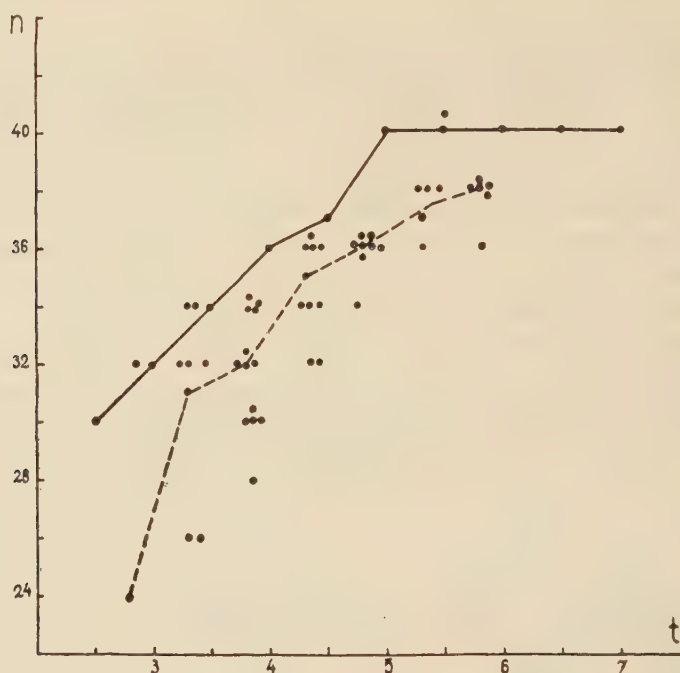


Fig. 15. — The  $n/t$  ratio curves; tabularium diameters ( $t$ ) — on abscissa, number of major and minor septa ( $n$ ) — on ordinate. Broken line and dots refer to *Hexagonaria laxa* Gürich (Dziewki, Givetian); continuous line — to *H. laxa jurkowicensis* Rozk. (Jurkowice, Givetian).

### B. Individual variations

Strong polymorphism, expressed in all the structural elements, is observable in the studied colony.

1. *Shape of corallites.* In cross section the shape of mature corallites varies considerably. Upon examining 14 calices the writer ascertained the following diameters (in mm):  $6 \times 8$ ,  $7 \times 8$ ,  $7 \times 11$ ,  $7 \times 12$ ,  $8 \times 9$ ,  $8 \times 10$ ,  $9 \times 10$ ,  $10 \times 10$ ,  $12 \times 12$ . Tabularium width ranges from 4 to 6.5 mm. The calicinal outline is usually roughly hexagonal, in a few cases heptagonal or trigonal.

2. *Tabularium/dissepimentarium ratio.* 120 mature corallites have been measured in order to correlate in longitudinal sections the tabularium width and its relation to the dissepimentarium. These correlation data are plotted in the graph of fig. 16, in which the  $t/\text{diss}$  correlation value is placed on the abscissa, the per cent number of individuals — on the ordinate. The



curve is distinctly asymmetrical, since the most frequent individuals are those with the ratio value at 1. This means equal width of the tabularium and dissepimentarium on either side of it. The per cent number of individuals,

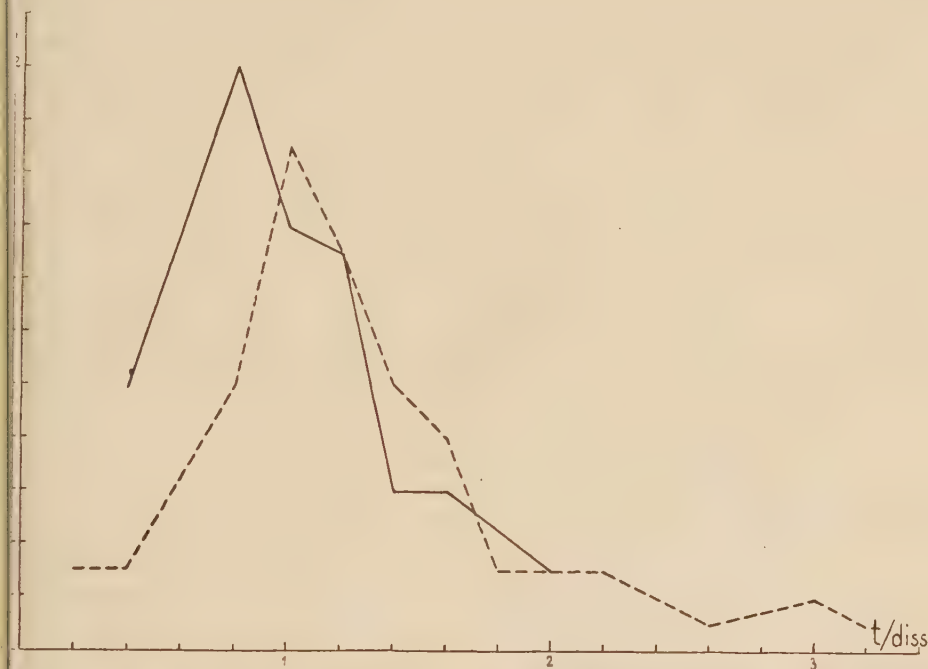


Fig. 16. — The  $t/diss$  ratio curves; tabularium ( $t$ ) to dissepimentarium ( $diss$ ) diameter ratio — on abscissa, per cent of specimens — on ordinate. Broken line refers to *Halysites laxa* Gürich (Dziewiki, Givetian); continuous line — to *H. laxa jurkowicensis* Rozk. (Jurkowice, Givetian).

which width of dissepimentarium exceeds that of the tabularium, is small (0.2—0.8). On the other side of the apex, however, the curve has a gentler slope, thereby raising this value to 3.2.

3. *Number of vesicular rows.* The number of the rows of vesicles varies conspicuously even within one corallite. Mature corallites only, not producing buds, have been taken into account by the writer. It is well known that new buds completely reduce the dissepimentarium and substitute it. Mature corallites with morphology not disturbed by budding processes, dissepimentarium variability is as shown in table 3.

These measurements have been taken with the use of a micrometer, under 50-fold microscopic magnification. Data tabulated here above indicate that dissepimentarium displays strong variations, there not being two identical places within one corallite. Dissepimentarium width varies on either side and, independently thereof, the number of dissepimental rows

Table 3

Dissepimentarium variability and number of vesicular rows

Corallite no.	Left dissepimentarium width (mm.)	Number of rows	Width of dissepiments (mm)	Right dissepimentarium width (mm)	Number of rows	Width of dissepiments (mm)
1	1.0	2	0.5 0.3	1.3	3	1.5 1.0 0.5
	2.5	4	1.0 0.5 0.5 0.3	3.0	4	1.4 0.8 0.6 0.4
2	2.5	6	1.5 1.0 0.8 0.8 0.5 0.4	2.0	4	0.7 0.6 0.5 0.5
	2.5	3	3.5 2.5 1.5	3.5	8	1.5 1.3 0.8 0.7 0.7 0.6 0.6 0.3
3	3.8	4	3.5 2.5 1.5 1.5	2.0	2	2.0 1.5

varies too. Variations of vesicle width occurs too, since large ones are present together with tiny ones.

4. *Number of tabulae in 2 mm.* Dissepimentarium width is controlled by the amount of space available for the growth of individual corallites within the corallum; the size and hence the number of dissepiments is affected by environmental conditions, while tabularia display some constancy. On the other hand, the position and arrangement of the tabulae varies strongly. Tabulae, similarly as dissepiments, are more plastic and probably depend mainly on exogenetic factors.

In order better to clear up this problem, the writer has measured about 30 mature corallites, thus ascertaining the following data: a) tabulae are

mostly convex or nearly flat, the presence of concave tabulae has been ascertained in four cases only; b) number of tabulae in 2 mm varies strongly, two tabulae over that distance is a rare occurrence, most frequently there are 5 or 6, this being the case in 50 per cent of the examined corallites; c) tabulae may be complete or incomplete. Those consisting of axial and triaxial parts and provided with supplementary plates predominate. Their occurrence is most irregular, since they have been encountered in very young corallites as well as in large tabularia. Moreover, wide-spaced, incomplete tabulae may occur side by side with vesicular ones.

5. *Numerical ratio of complete septa to septa subject to reduction.* The characteristic feature of *Hexagonaria laxa* is the splitting up of some septa into mature calices into radial segments. A short conical base of the reduced septum always persists on the peripheral wall. This rudiment is of the same length as minor septa. The farther septal segments are placed on dissepiments. Occasionally only the peripheral base of the major septum and its axial end on the inner pseudotheca are present. These two extreme ends never disappear. Minor septa, if somewhat longer, are likewise reduced to a short row of radiate spines which, however, never protrude beyond the peripheral wall. In order to ascertain the number of septa, it has been found most convenient to count the axial ends of major septa, since the number of minor septa is always the same as that of the major.

The number of septa subject to reduction varies strongly. This depends on the presence of large dissepimental vesicles in a wide dissepimentarium, since it is there that the buds arise. The septal spines constitute the initial stage preparing space for budding, hence they are a caenogenetic character. The number of septa subject to reduction has been counted by the writer in 55 calices. The obtained data are given in table 4.

Table 4  
Variability in number of reducing septa

Total number of major septa	Number of septa subject to reduction in calices										
	0	1	2	3	4	5	6	7	8	9	10
19	3	1	—	1	2	—	—	1	1	1	—
18	2	1	2	3	3	1	1	1	1	1	1
17	1	1	1	—	—	—	1	2	2	1	1
16	2	—	1	—	2	2	1	—	—	—	—
15	5	—	—	—	—	—	—	—	—	—	—

Exclusively complete septa occur only in 25 per cent of the examined calices, provided with 15—19 major septa. Calices with 18 major septa contain the highest per cent (33) of reduced septa.



6. *Septal thickness.* Septa are a structural element exhibiting notably strong variability. Thickness is one of the variable features. In the neanic stage septa are broad in section, gradually narrowing towards the axis. In mature corallites we note great diversity in this respect, each septum of any one part of the corallite being different. About 200 septa have been measured by the writer in sections of corallites from one colony, with the use of the micrometer under a 50-fold magnification. The obtained data show that on the whole peripheral bases of septa are as follows:

Thickness (in mm)	Per cent of septa
0.10 - 0.12	6
0.14 - 0.16	40
0.18 - 0.24	37
0.26 - 0.40	17

Similarly dilated septa occur in the inner pseudotheca, being those which, together with the inner whorl of dissepiments, form this wall. The following data have been ascertained by the writer:

Thickness (in mm)	Per cent of septa
0.10 - 0.12	3
0.14 - 0.16	22
0.18 - 0.24	39
0.26 - 0.40	34
0.40 - 0.60	2

Data tabulated above show that septa attain on the average greater thickness within the inner wall than on the peripheries. Thus, septa with thickness of 0.18—0.40 mm predominate in the wall (73 per cent), while those of 0.14—0.24 mm are most frequent at the base (77 per cent).

Besides the two most conspicuous dilations septa may show several constrictions or even gaps. In 5 per cent of septa the most constricted places are 0.02 mm thick, in 75 per cent 0.03—0.08 mm, while in 20 per cent the most constricted places do not much differ from the unconstricted parts and are 0.1—0.19 mm thick.

7. *Number of carinae on septa.* The examination of this character presents some difficulties since the carinae are very fragile. On some septa where they lie opposite, they are distinct, on others where alternating, they may be hardly discernible, so that septal sinuosity or dilations only indicate their presence. Dissepiments are attached to carinae, these are most conspicuous along thin septa and when the thin walls of vesicles are added to the bead-like dilations. 170 septa have been minutely examined by the writer, showing that 13 per cent are without carinae, 20 per cent have on

or two pairs of carinae, 50 per cent have 3—4 pairs, while 17 per cent are provided with as many as 5—8 pairs. The Dziewki form differs from the Jurkowice variety in lack of conspicuous carinae.

8. *Septal length*. 140 septa have been measured; the obtained data show that major septa vary strongly in length, the longest being 3.2 mm, the shortest 0.6 mm. As usual, mature calices only have been measured. Minor septa are considerably shorter, ranging from 0.06 to 0.64 mm. The length ratio of the major to minor septa is shown here below:

Per cent of examined septa	Major/minor septal length
25	3 - 4
60	5 - 8
15	9 - 11

The following are the most frequent figures of length (in mm):

Major septa	Minor septa
2.72	0.54
2.48	0.48
1.76	0.32

Notably long major septa, 9 or 10 times as long as the minor, are very rare. E. g.

Major septa	Minor septa
3.00	0.35
2.56	0.24
2.07	0.19

The Dziewki form is characteristic foremost by extremely short minor septa. This suggests an obvious tendency to reduction.

*Hexagonaria laxa jurkowicensis* n. subsp.

(fig. 15-19)

*Material*. — Two subcircular colonies, 9 cm in diameter, from a stromatoporoïd-tabulate reef in Jurkowice near Opatów.

*Diagnosis* of holotype (fig. 17-19, microscopic sections 14 and 16). — This variety of the species *H. laxa* differs from the type form in larger calices (largest one 16 × 18 mm), slightly broader tabularium (up to 7 mm in diameter), and greater number of septa. In mature calices there may occur as many as 20 major septa, tending to break up into short irregular segments. All septa are conspicuously carinate. Trabeculae thick (0.16 mm), budding intermural.



Fig. 17. — *Hexagonaria laxa jurkowicensis* Rozk.; Jurkowice, Givetian. Cross section of a cerioid colony (slide no. 14).



Fig. 18. — *Hexagonaria laxa jurkowicensis* Rozk.; Jurkowice, Givetian. Longitudinal section of a cerioid colony (slide no. 15).

### A. Blastogeny

1. *Development of bud.* Longitudinal section shows that budding is more frequent here than in the Dziewki form. Many buds are produced growing subradially from some central corallite at an angle of  $70-80^\circ$ . Their further development is similar to that in *H. laxa* (fig. 17).

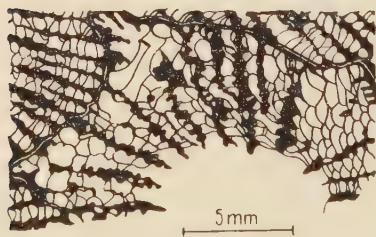


Fig. 19. — *Hexagonaria laxa jurkowicensis* Rozk.; Jurkowice, Givetian. Cross section of a part of corallite with bud in the neponic stage; new epitheca still lacking (slide no. 16).

2. *The n/t ratio variations during ontogeny* (fig. 15). Correlation of the number of septa with the tabularium width and its ontogenetic variations are shown in table 5.

Ms coefficients of the two forms, from Dziewki and Jurkowice, are very similar, being 7.9 and 8.3 respectively. The slightly higher figure in the Jurkowice variety is due to the greater number of septa there.

40 septa continue to be present throughout 5 classes, beginning with the tabularium diameter at 5-7 mm. This indicates distinct tendency for the diameter growth to dominate over the numerical increase of septa. The correlation curve placed near the n/t ratio line of the Dziewki form (fig. 15)



Table 5

Mean number of septa (Mn) and mean diameter of tabularium (Mt) ratio with respective coefficients (Mc, Ms)

Classes	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10
Mn I, II	30	32	34	36	37	40	40	40	40	40
Mt	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0
Mc1-Mc10	12.0	10.7	9.7	9.0	8.2	8.0	7.1	6.7	6.1	5.7
Ms n/t = 8.3										

suggests similarities in character. The only deviation consists in the numerical increase of septa during the ephebic stage of the Dziewki form, while in the Jurkowice form there is no variation in this respect.

Individual variations

Differences are very strong in mature forms. The contour of the corallite is roughly polygonal. The maximum corallite diameter in an exact cross section is 18 mm.

1. The tabularium/dissepimentarium ratio (fig. 16) comes close to that of the Dziewki form, as is shown by the correlation curve running parallel to the t/diss curve of the Dziewki form (fig. 16). Their course is analogous, but the summits are placed in different classes. The majority of the Dziewki specimens are with the t/diss ratio = 1, while in the Jurkowice colony that value is slightly lower (0.8). It has been ascertained that 46 per cent of the specimens have the tabularium narrower than the dissepimentarium. The evolutionary trend is to enlarge the colony by dissepimental growth.

Table 6

Dissepimentarium variability and number of vesicular rows

Corallite no.	Left dissepimentarium width (in mm)	Number of rows	Right dissepimentarium width (in mm)	Number of rows
1	6.5	8	5.0	9
	3.5	5	2.0	3
	2.1	4	1.0	2
	1.0	2	0.5	2
2	3.5	6	5.3	8
	3.2	5	2.5	5
	2.5	3	2.0	3
	1.0	2	0.6	1

2. *Number of vesicular rows* (fig. 18). This character varies strongly. It does not correlate with dissepimentarium width, but is strictly connected with the size of vesicles and, most likely, it is merely a function of outer environmental conditions (see table 6).

3. *Number of tabulae in 2 mm*. This is a strongly variable feature, as in the Dziewki topotype. Number of tabulae ranges from 2 to 6 in 2 mm. Tabularia with only 2 tabulae in 2 mm are unusual. Closely spaced tabulae are the most frequent, the majority being complete.

4. *Complete and reducing septa*. In mature calices, with a well developed dissepimentarium (fig. 17), septa begin to break up into segments. A short base invariably persists on the periphery, farther segments have yard-arm carinae united by thin stereozone strips. Upon further reduction, trabecules loose their junctions so that shapeless septal segments only persist comprising several conspicuous carinae covered by stereoplasm. In *H. laxa* they break up according to another pattern. There the septum separates into thin, slender septal spines fixed on the arched dissepimental wall. The peripheral bases of septa in the Jurkowice variety are then short, hardly discernible, but the axial ends are complete and strong, as in the topotype.

Similarly as in *H. laxa*, the number of regressive septa in the several calices varies. The number of reducing major septa ranges from 0 to 19. The same septum may disintegrate once or as many as six times (see table 7). The disintegration of septa into elongated parallel segments is rather frequent. Moreover, it has been ascertained that minor septa, though still slightly longer than in the topotype, are reduced more rapidly than the major septa. Analogously accelerated reduction is observable in the Dziewki form also.

Table 7

Numerical data showing interrelation of calyx diameter and septal disintegration

Calyx no.	Calyx diameter (mm)	Tabularium diameter (mm)	Number of major septa	Separation			Number of complete septa	Disintegration into elongated segments
				one-fold	two-fold	three-fold		
1	17.0	7.0	20	12	6	—	2	10
2	13.0	7.0	20	5	2	2	11	1
3	10.0	5.5	20	1	—	—	19	—

As is shown in the above table, which illustrates three haphazardly picked out mature calices, progressive septal regression is associated with size of calyx.

5. *Septal thickness* (fig. 17). Septa here show notably stronger structure than those in the type form, as well as greater diversity of thickness: distinctly spindle-like ones occur together with slender ones, which have rounded carinae and the appearance of a string of beads.

For the sake of comparison the writer has measured, with the use of a micrometer under 50-fold magnification, the septal thickness at the peripheral base, in the inner pseudotheca and in places of greatest constriction. On these measurements it has been established that:

a) minimal basal thickness = 0.3-0.4 mm in 15 per cent of septa, most frequent thickness = 0.5-0.8 mm in 62 per cent, and maximum thickness = 0.9-1.3 mm in 23 per cent of septa;

b) as regards thickness within the pseudotheca, measurements show that the peripheral base of septa and the periaxial dilations have similar value, i.e. that in these two points the septa are analogously dilated. In the Jurkowice form these dilations are stronger, but the two above mentioned, equally strong thickenings, occur in the toptype too:

	<i>Hexagonaria laxa</i>	<i>H. laxa jurkowicensis</i>
Dilation at base	0.1 - 0.4	0.3 - 1.3
Dilation within inner pseudotheca	0.1 - 0.6	0.5 - 1.3

Thread-like connections of the lumpy trabecules are as fine as those in the type form where the sharp-pointed end of septal spines makes its appearance. The narrowest constrictions range from 0.03 to 0.08 mm and are not rare.

6. *Number of carinae on septa* (fig. 19). The Jurkowice variety is provided with markedly conspicuous carinae, readily observable in transverse and longitudinal sections. The opposite arrangement predominates, the alternating pattern is less common. Dissepiments, strongly dilated in the periaxial part of the corallite, are attached to the processes of carinae.

Upon measuring 50 septa, it is possible to describe the numerical occurrence of carinae on septa. Some septa are without distinguishable carinae. If so, the trabecules are mutually closely connected throughout their length by stereoplasm. On other septa carinae are conspicuous. Their number varies. Septa, provided with 5—6 pairs of carinae each, are frequent, the majority have 9 pairs, but occasionally 13, 15 or even 17 pairs may occur. In the Dziewki form 3—4 pairs of carinae are the most frequent, while 5—9 pairs on one septum is the maximum recorded number.

7. *Septal length*. Length correlation of major and minor septa in the Dziewki form differs completely from that in the Jurkowice form. Minor septa are considerably longer in the Jurkowice colony, nearly reaching to



the inner wall. Figures relating to length of both septal types are as follows: in 70 per cent of septa the sI/sII ratio = 1.1-2. This means that major septa are either only slightly longer than, or twice the length of minor septa. In *H. laxa* from Dziewki, however, the sI/sII ratio = 5-7-9, with the predominance of calices having septa as many as nine times the length of minor septa.

### C. Comparison with the type form

Morphology, microstructure, ontogeny and individual variability of two closely allied forms have been investigated: i.e. the Dziewki topotype *H. laxa* and the variety *H. laxa jurkowicensis* from Jurkowice. The two forms come from similar environments in a tabulate-stromatoporoid reef.

1. Characters in common have been ascertained providing evidence for assignment of both forms to the *H. laxa* group. They are with similar structural pattern and similar ontogeny. The latter is indicated by arrangement and development of buds, and correlation curves of the same type. Individual variability displays analogous tendencies.

2. Differences, however, occur reasonably suggesting separation into a variety. They are as follows: shape of colony is tabular in the type form, but subcircular in the Jurkowice form. In the type form buds grow vertically upward, in the latter — latero-radially. In the variety budding is frequent. Calices attain the size of  $16 \times 18$  mm in the Jurkowice variety, as compared against  $12 \times 12$  mm in the Dziewki form. The tabularium has a greater mean diameter, attaining the maximum figure of 7 mm against 6 mm in the Dziewki corallites. Septa more numerous and rapidly stabilized. All skeletal elements more massive. Septal regression is expressed in the Jurkowice form in more robust and more closely spaced numerous carinae and in the separation of septa into numerous thick lumps. The inner wall is less compact in the Jurkowice variety.

3. Greater diameter of calyx, greater number of septa, and more advanced reduction of the septal system indicate more advanced phylogeny, as compared with the type species. Hence the writer regards the Jurkowice form as a mutation.

4. Another morphological difference confirms the supposition that the Jurkowice variety cannot be a straight line descendant of the type form, but merely belongs to the *H. laxa* group. It consists in the considerable constant length of the minor septa in the Jurkowice colony throughout all the ontogenetic stages, while in the type form the septa are mostly short. Although the tendency for septal reduction mainly involves minor septa, nevertheless in the Jurkowice variety they nearly always remain long

through the later ontogenetic stages. The original structural pattern here is, therefore, somewhat different and the evolutionary trend in this respect has a different degree of intensity.

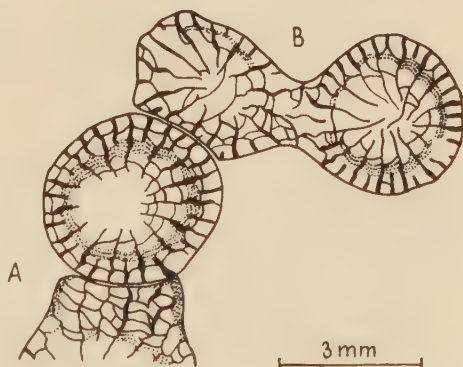
*Peneckiella minor* (Roemer) *kunthi* (Dames)

(fig. 20-29)

869. *Cyathophyllum kunthi* Dames; W. Dames, Herr Dames an..., p. 699.  
 873. *Fascicularia kunthi* Dames; W. N. Dybowski, Beschreibung zweier aus Oberkunzendorf..., p. 406 - 408, pl. 13, fig. 3, 4.  
 881. *Fascicularia kunthi* Dames; C. Schlüter, Über einige Anthozoen..., p. 104.  
 885. *Cyathophyllum kunthi* Dames; F. Frech, Die Korallenfauna..., p. 35 - 36, pl. 1, fig. 4 a - b.  
 895. *Disphyllum* (*Phacellophyllum*) *caespitosum* (Goldf.), partim; W. D. Lang & S. Smith, *Cyathophyllum*..., p. 573.  
 899. *Macgeea* (*Thamnophyllum*) *caespitosum* (Goldf.) var. *minus* (Roemer), partim; A. v. Schouppé, Die „Thamnophyllen“..., p. 154 - 155, pl. 11, fig. 38 - 39.  
 956. *Macgeea* (*Thamnophyllum*) *kunthi* (Dames); H. Flügel, Kritische Bemerkungen..., p. 360 - 361.  
 957. *Thamnophyllum kunthi* (Dames); M. Rózkowska, Considerations..., p. 84, fig. 1 A; p. 100, fig. 10; p. 140.

**Material.** — Reef built up of phaceloid colonies of this species and of dendroid colonies of *Sudetia lateseptata*, all cemented by dark bituminous oogenic limestone. South shore of Daisy Pond near Mokrzyszów, Upper Frasnian. 34 thin slides have been cut with transverse and longitudinal sections.

Fig. 20. — *Peneckiella minor kunthi* (Dames); Mokrzyszów, Upper Frasnian. Cross sections of mature corallites: A corallite coalesces with neighbour by its elongated part, B rud in contact with parent corallite (slide no 35).



**Diagnosis.** — Phaceloid colony; corallites straight, covered by thick epitheca, locally touching. Diameter 2.5 to 4.8 mm. Number of septa ranging from  $12 \times 2$  to  $16 \times 2$ , only exceptionally  $18 \times 2$ . Major septa long with blunt axial ends, thick and zigzagged, within the dissepimentarium frequently carinate. Minor septa short. Double row of diversely shaped dissepiments

(horizontal, horse-shoe, sigmoidal, peneckielloid). Tabulae usually complete, horizontal or concave. Trabecular fans, trabeculae thick (0.08—0.16 mm). Budding latero-thamnophylloid.

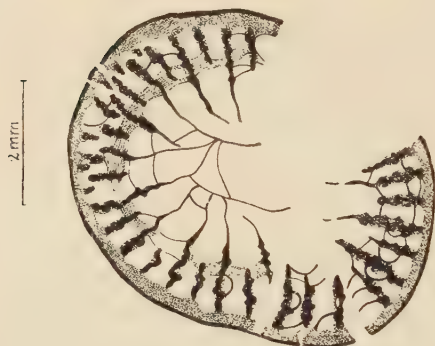


Fig. 21. — *Peneckiella minor kunthi* (Dames); Mokrzyszów, Upper Frasnian. Cross section of a corallite with distinctly carinate septa, frequently not surrounded by stereoplasm (slide no. 41).



Fig. 22. — *Peneckiella minor kunthi* (Dames); Mokrzyszów, Upper Frasnian. Longitudinal section of a corallite (slide no. 22).

#### A. Blastogeny

1. *Development of bud* (fig. 23—25). The above named species produces lateral buds, arising from the dissepimental tissue of the budding corallite. Similar mode of budding occurs in *Thamnophyllum caespitosum* (Goldf.). In the latter form the bud bends at a right angle, in the Mokrzyszów form — at 45°. During the early stage (fig. 23) some of the major and minor septa of the parent corallite grow longer and become part of the bud's septal

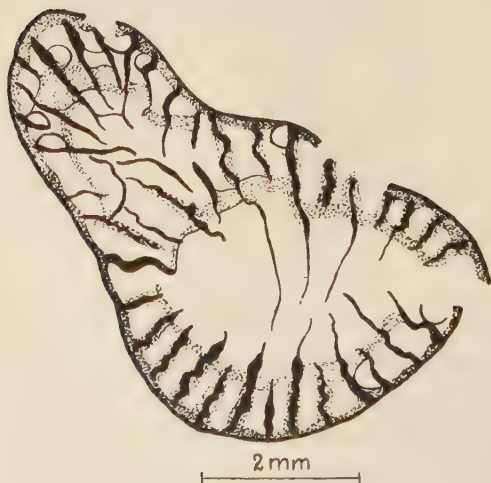


Fig. 23. — *Peneckiella minor kunthi* (Dames); Mokrzyszów, Upper Frasnian. Cross section of corallite with bud: elongated septa of parent corallite enter the bud (slide no. 35).



apparatus resting on the outer and the periaxial side in relation to the budding polyp. This is thamnophylloid lateral budding not common in the *thamnophyllum* lineage. It is distinguishable from lateral buds of the sphylloid type where septa of the parent corallite persist on the outer side of the bud (fig. 4, 5).

During the following stage (fig. 24), with diameter of 2.5 mm, the bud is provided with a completely developed interior pseudotheca, but the epitheca never separates the bud from the parent corallite.

In longitudinal section (fig. 25) the bud is seen to arise from the dissepimental tissues consisting of normal vesicles and horse-shoes. During the primary stage the structure is diaphragmatophoric. On the outer side of the bud is the epitheca, absent from the inner side, hence the bud there is directly united with the parent corallite.

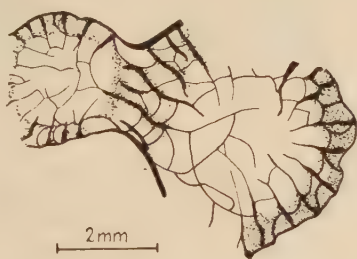


Fig. 24. — *Peneckiella minor kunthi* (Dames); Mokrze-szów, Upper Frasnian. Section of a bud with complete pseudotheca (slide no. 10).

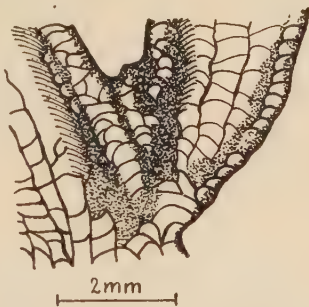


Fig. 25. — *Peneckiella minor kunthi* (Dames); Mokrze-szów, Upper Frasnian. Longitudinal section of a bud; lack of epitheca between two corallites (slide no. 16).

2. *The n/d ratio variations during ontogeny* (fig. 26). In the neanic and ephyonic stages septa increase rapidly, the diagram curve rises almost steeply. During the ephybic stage, with diameter of 3.4 to 4.4 mm, the number of septa is already constant and the morphogeny complete. A slight increase in the calicinal diameter occurs only.

3. *Septal length* (fig. 26) varies distinctly. In young individuals septa are long, in the axis of the corallite nearly mutually coalescent. During further growth of bud septa diminish conspicuously. The c/d correlation curve shows changes during ontogeny within the axial portion without septa. This area expands nearly uniformly with the increase of the corallite diameter. With diameter of 2.4 to 3.9 mm the corallite centre, not provided with septa, is minute (0.3—0.5 mm), later widening up to an average of 1 mm in the largest specimens.



Fig. 26. — *Peneckiella minor kunthi* (Dames); Mokrzezów, Upper Frasnian. Ratio curve of total septal number ( $n$ ) and corallite diameter ( $d$ ), also with ratio curve of axial area ( $c$ ) free of septa and corallite diameter ( $d$ );  $c$ ,  $d$  — in mm.

### B. Individual variability

Individual variability is strong. It is most conspicuously expressed in regressive elements, such as dissepiments and septa. Tabulae vary considerably too.

1. *Dissepimental structure* (fig. 27-28). Dissepimentarium extremely narrow, involving one, never more than two vesicular rows. Dissepiments vary notably in shape and dimensions, the following types being distinguished: a) small horse-shoe dissepiments with both arms resting on the underlying vesicle; the symmetry line of the trabecular fan occurs at the uppermost part of the vesicle; b) „horizontal” dissepiments, in this species slightly arched upward, occur outside the horse-shoe dissepiments; in some places they are missing near the horse-shoe, in others may be underlain over the entire width; c) normal, „peneckielloid” dissepiments, distally flattened, are

most common and the largest; their inner arm rests on the underlying vesicle, the outer one enters the thick wall; it does not, however, participate in its formation, but seemingly leans against it; d) another, rather rare dissepimental type is that apparently due to the fusion of two distinct vesicles: horse-shoe and the horizontal; in shape it is sigmoidal (fig. 27).

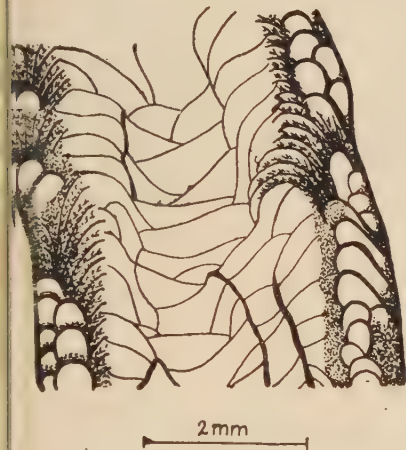


Fig. 27. — *Peneckiella minor kunthi* (Dames), Mokreszów, Upper Frasnian. Longitudinal section showing horse-shoe dissepiments, peneckielloid, horizontal and sigmoidal vesicles; trabecular fans resting on horse-shoe dissepiments or on normal (peneckielloid) vesicles (slide no. 40).



Fig. 28. — *Peneckiella minor kunthi* (Dames); Mokreszów, Upper Frasnian. Longitudinal section showing various dissepiments (slide no. 25).

The disappearance of horse-shoe dissepiments calls for closer attention, since — together with the symmetric trabecular fans — they constitute the most characteristic features of the *Thamnophyllidae*. The symmetry line of the trabecular fans is shifted towards the epitheca together with the extinction of horizontal dissepiments. Although both the horse-shoe and the horizontal dissepiments become obsolete, trabecular fans persist and continue to occur in the descendant form *Sudetia lateseptata* n.sp.

2. *Peneckielloid and horse-shoe dissepiments*. Peneckielloid vesicles terminate over horse-shoe dissepiments. Through the investigation of their numerical occurrence in 40 corallites, involving 20 dissepiments, the following data have been obtained by the writer: in one third of the examined corallites the number of peneckielloid dissepiments slightly exceeds that of the horse-shoe type, the ratio being 2 : 1; in another third of the corallites the peneckielloid type is three or four times as numerous, while in the remaining 37 per cent its number is five to seven times that of the horse-shoe type. This indicates rapid extinction of thamnophylloid characters. More-



over, observations confirm that the part played by horse-shoe dissepiments in the formation of dissepimentarium is not at all connected with ontogenetic age.

3. *Septal thickness* is a feature not controlled by age, and strongly variable throughout ontogeny. Thin septa may occur together with the spindle-like type even in the youngest corallites. Their maximum thickness ranges from 0.08 to 0.32 mm. In the same mature calyx we may encounter thin, wide spaced septa, together with those inflated to such an extent by the superimposition of stereoplasm that their width is two or three times greater. Septa have been measured at their maximum width, within the inner wall. The fracture lines there distinctly separate the septum from the inflated vesicular wall touching them. This observation is illustrated by the following numerical data (in mm):

Diameter of calyx	Thickness of major septa
2.5 - 2.7	0.09 - 0.32
3.0 - 3.9	0.09 - 0.32
4.0 - 4.5	0.08 - 0.32

4. *Septal carinae*. The presence of carinae in this species has been ascertained without doubt. Outside they are not always discernible, being masked by the stereoplasm. Septa are then broad, spindle-like; carinae most conspicuous (fig. 21) when reduction of stereoplasm has occurred. Schouppé (1958, p. 230), when stating the generic diagnosis of *Peneckiella* (based on the genotype *Diphyphyllum minus* Roemer), writes that „septae are not distinctly carinate”. In her diagnosis of the newly established genus *Peneckiella*, with genotype as mentioned above, Soshkina (1939, p. 23) postulates that „septae are zigzagged and occasionally provided with few septal carinae”. Three possibilities are suggested on the Mokrzyszów specimens with macro- and microstructure elements occasionally excellently preserved: a) thin non carinate septa, b) septa thickened, carinae indistinct, c) strongly carinate septa. In microscopic sections of the Grund genotype microstructure is not readily discernible. Thin as well as thicker, spindle-like septa occur; carinae are indistinct, like in some Mokrzyszów specimens. The presence of carinae in the Mokrzyszów specimens indicates the maturity of the corallite; in corallites with diameter of up to 2.8 mm septa and the trabecular line are straight. Beginning with a 3 mm diameter septa may be zigzagged, but without distinct carinae. With diameter from 3.7 mm upwards carinate septa make their appearance. Their number varies; carinae are either completely lacking or occur on 1-3 septa, occasionally on as many as seven septa.

5. *Spacing of tabulae*. The arrangement of tabulae is not affected by ontogenetic age, being rather a function of environmental conditions. Two

cardinal types of tabulae occur: a) closely spaced, horizontal, with a slight bowl-like depression in the axial area, usually complete (fig. 29) and b) complete, deeply concave, widely spaced (fig. 27-28). In type a) 9-12 tabulae fit into 2 mm, in type b) there may be from 4 to 7 tabulae in 2 mm.

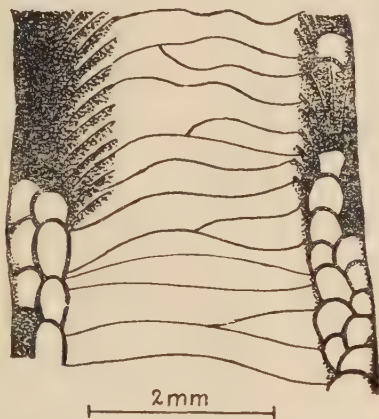


Fig. 29. — *Peneckiella minor kunthi* (Dames); Mokreszów, Upper Frasnian. Longitudinal section showing various dissepiments and closely spaced, horizontal tabulae (slide no. 21).



Fig. 30. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Cross section of a corallite; minor septa nearly completely reduced (slide no. 12).

**Remarks.** A comparison of the Mokreszów form with sections of the und genotype shows very close similarities; it is in fact hardly possible to distinguish forms from these two localities. Since the author is not familiar with the variation range of the species *P. minor*, she postulates that the Mokreszów form is a geographical variety. It is characterized by fewer septa with corresponding calicinal diameter ( $16 \times 2$  septa in the Mokreszów form against  $18 \times 2$  septa in *P. minor*, with diameter of 3.6 mm).

#### Genus *Sudetia* n. gen.

#### *Sudetia lateseptata* n. sp.

(fig. 30 - 43)

**Material.** — Large irregularly dendroid colony ( $9 \times 15 \times 6$  cm), also numerous small fragments cemented in dark bituminous Upper Frasnian limestone of Mokreszów, accompanied by *Peneckiella minor kunthi*. 15 thin sections have been prepared with transverse and longitudinal sections.

**Diagnosis** (holotype, fig. 30-33, microscopic sections nos. 12, 15). — Dendroid colony with zigzag corallites provided with 32-36 major and minor septa, at diameter of 3.0 to 4.6 mm. Thick epitheca, conspicuous inner pseu-

dotheca occurring on the boundary line between the tabularium and the dissepimentarium. Calyx deep, with flat bottom and steep walls, completely surrounded by the epitheca as far as the distal end of septa. Major septa short, spindle-like, mostly touching laterally, with wide carinae usually covered by stereoplasm; minor septa of varying length, often com-

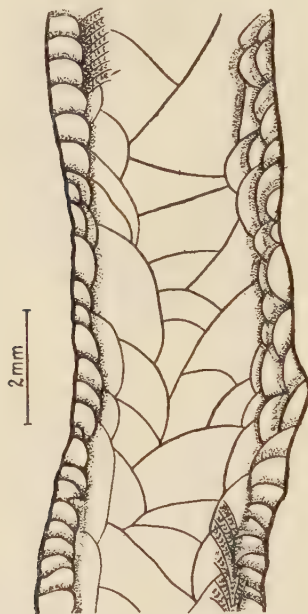


Fig. 31. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Longitudinal section (slide no. 23).



Fig. 32. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Longitudinal section (slide no. 12).

pletely reduced. One row of flattened peneckielloid dissepiments. Tabulae mostly complete, concave or horizontal. Trabecular fans asymmetrical, with the divergence line near to the wall, resting on the distal end of a peneckielloid vesicle. Trabeculae thick (0.06-0.18 mm). Two modes of budding: either lateral, thamnophylloid, rather rare, or syringoporoid, with aseptal and brevisseptal stages, most common. Numerous connecting processes.

#### A. Blastogeny

1. *Development of bud* (fig. 34-42). The corallite frequently produces processes. Some (left side, fig. 33), involving dissepiments as well as tabulae, are connecting processes, others inclining from the mature corallite at an angle of  $45^\circ$ , are buds filled by large vesicles responsible for their cystiphylloid appearance.

The following stages are distinguishable during syringoporoid blastogeny:



a) Stage I (fig. 34, 35) — in cross sections septa lacking in the bud which, together with the parent corallite, is enclosed in a common epitheca. Septa of a mature individual are not introduced into the bud, which contains only widely spaced dissepiments and tabulae. This aseptal stage continues until the bud attains a diameter of 2 mm. In fig. 35 one side of the bud touches the adjacent corallite.

b) Stage II, brevisseptal (fig. 36, 37) — septa present in buds with diameter from 0.8 to 2.8 mm. In this stage, common in thin slides, beginning major septa are discernible. In fig. 36 the young bud coalesces with *Peneckiella minor kunthi*, being on this side provided with 3 short septa. The bud is provided with the epitheca and tabulae. The same thin slide shows a brevisseptal bud, slightly older, already with 16 short thin major septa, some of which probably belong to the minor group. The inner pseudotheca and the dissepimentarium have been formed. The bud is attached with a process to *P. minor kunthi* (fig. 37).

c) Stage III — with 14-16 major septa which are thick, zigzag (fig. 38), with short minor septa locally intervening. Bud 2.5 mm in diameter, coalescing with *P. minor kunthi*. Fig. 39 shows distinctly syringoploid budding. The bud arises from the transversely cut parent corallite with short, thick major septa and partly reduced minor septa. It is thick-walled, and provided with large vertical vesicles. Septa of the budding corallite are not introduced into the bud. Normal peneckielloid dissepiments make their appearance at diameter of 2.4 mm. Eight zigzag major septa, with thickness uniform throughout the length, are seen on the distal end of bud. Their axial ends hardly protrude beyond the inner wall. Several minor septa occur too. Complete and incomplete tabulae present. A short and broad trabecular fan (fig. 39) observable on the convex wall of the vesicle.

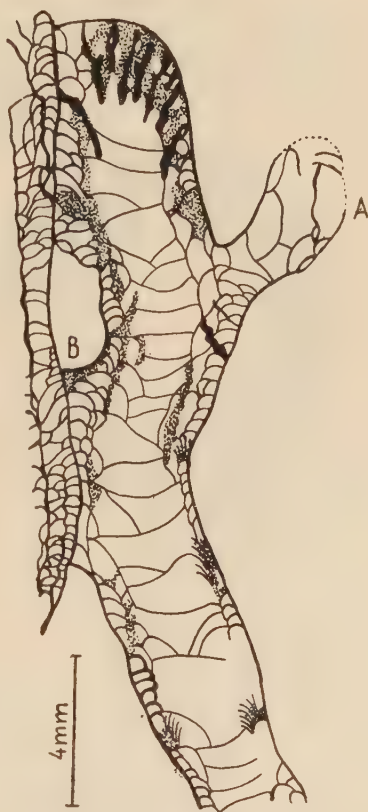


Fig. 33. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Longitudinal section showing shape of corallite with syringoploid bud (A) and connecting process (B) (slide no. 15).

Lateral, thamnophylloid budding (fig. 40), as in *P. minor kunthi*, less common, may occur together with syringoporoid budding. In the thamnophylloid type septa of the parent corallite elongate to attain the interior of the bud, and form short septa on the outer and inner bud wall. The epitheca



Fig. 34. — *Sudetia lateseptata* Rozk.; Mokrzyszów, Upper Frasnian. Cross section of a corallite with aseptal bud (slide no. 12).



Fig. 35. — *Sudetia lateseptata* Rozk.; Mokrzyszów, Upper Frasnian. Cross section of a budding corallite with aseptal bud, slightly obliquely cut (slide no. 47).

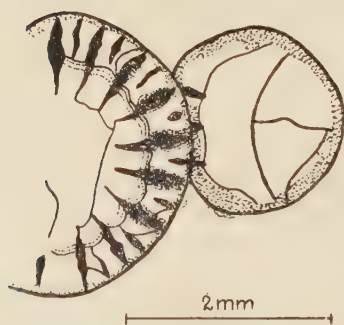


Fig. 36. — *Sudetia lateseptata* Rozk.; Mokrzyszów, Upper Frasnian. Bud with three septa, touching the adjacent corallite; both in cross section (slide no. 51).

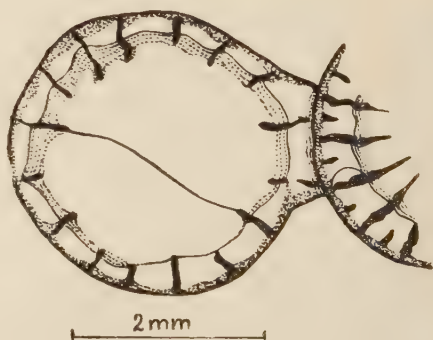


Fig. 37. — *Sudetia lateseptata* Rozk.; Mokrzyszów, Upper Frasnian. Bud slightly more developed, brevisseptal stage with connecting process (slide no. 51).

does not, however, separate the bud from the parent corallite, the two individuals are intimately connected in both types of budding.

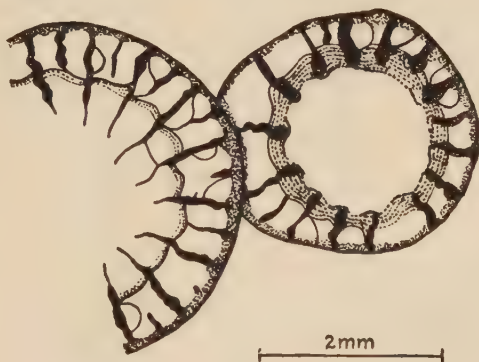


Fig. 38. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Young individual in neanic stage, touching the adjacent corallite (slide no. 51).



Fig. 39. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Budding corallite with a bud, in longitudinal, slightly oblique section (slide no. 52).



Fig. 40. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Thamnophylloid budding, elongated septa of budding corallite enter the bud (slide no. 50).



In the same thin slide we can also see young individual corallites possibly the equivalents of oozoids. From the very beginning (fig. 41), with diameter of 1 mm, they are provided with major septa as well as with large vesicles and complete tabulae. Several major and minor septa, divided into radiating segments, occur on the distal, somewhat obliquely cut end



Fig. 41. — *Sudetia lateseptata* Rozk.; Mokrzezów, Upper Frasnian. Juvenile corallite, probably an oozoid, provided with septa in the earliest stage, at the very base (slide no. 52).



Fig. 42. — *Sudetia lateseptata* Rozk.; Mokrzezów, Upper Frasnian. Juvenile corallite, probably oozoid, in longitudinal, slightly oblique section, with cystiphylloid bud at the distal end (slide no. 54).

An interpretation of the young corallite in fig. 42 presents some difficulty. It is probable that a larva, secreting a calyx with septa, 1.5 mm in diameter, has been attached to a mature corallite of *Sudetia lateseptata*.

A cystiphylloid aseptal bud arises from the young corallite even with diameter of only 2 mm.

Remarks. Soshkina (1954, p. 36, pl. 5, fig. 2), when describing *Penec-  
tiella jevlanensis* Bulvanker from Livonian strata of the Russian Platform,  
mentions buds occurring in the form of cystiphylloid vesicles. At a diame-  
ter of 1.5 mm these buds are without septa, their beginnings only being  
discernible as short spines on the wall. Similar buds have been ascertained  
by Soshkina (1954) in *Donia rossiensis* Soshkina, in Upper Frasnian beds.

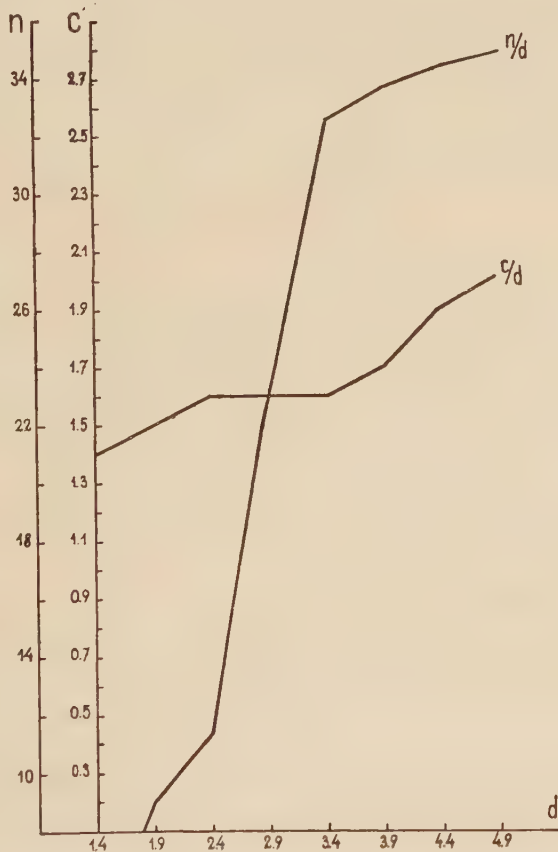


Fig. 43. — *Sudetia lateseptata* Rozk.; Mokreszów, Upper Frasnian. Ratio curve of total septal number ( $n$ ) and corallite diameter ( $d$ ), also width ratio curve of axial area ( $c$ ) free of septa and corallite diameter ( $d$ );  $c$ ,  $d$  — in mm.

The above mentioned species of that author may possibly be referable to the same group as *Sudetia*, inasmuch that they display similarities of structural pattern and of microstructure.

2. *Ontogenetic variations in the number of septa* (fig. 43). 62 corallites in various ontogenetic stages have been examined for the  $n/d$  ratio. The number of septa is shown to increase rapidly during the neanic stage, with

diameter of up to 3.4 mm. Major and minor septa may be as many as 32. From that point on, during the ephebic stage, major and minor septa together attain slowly the number of 34. The frequent loss of minor septa in mature corallites has not been here taken into account.

3. *Width variations of axial aseptal area.* The c/d ratio, i.e. diameter of axial aseptal area (c) and diameter of corallite (d), similarly as the n/d ratio, is strictly governed by the stage of ontogeny. During the aseptal stage the whole interior is free of septa. Later, short septa appear and elongate rapidly. The axial area free of septa hardly augments at all at diameters ranging from 1.4 to 3.4 mm. During the ephebic stage septa still continue to grow, but slowly, as is shown by the following numerical data (in mm):

Diameter	Septal length
1.4	—
2.4	0.4
3.4	0.9
4.4	1.3
4.5	1.3

4. *Development of septal carinae dependent on ontogeny.* In young individuals (with diameter of up to 3.4 mm), the septa are thin, zigzag, and the whole interior is filled by a dark bituminous substance; carinae are not discernible although uncovered by superimposed stereoplasm. In mature specimens, however, 6 to 9 conspicuous, distinctly separated trabeculae are discernible in practically every septum, usually masked by stereoplasm. When the stereoplasm disappears, trabeculae grow more distinct in the form of carinae on septal edges.

#### B. Individual variations

In mature individuals skeletal elements vary strongly. The variation here involves shape of corallite, size and arrangement of dissepiments, spacing and structure of tabulae, thickness of septa and reduction of minor septa.

1. *Shape of corallites* varies largely, as is shown in cross and longitudinal sections. They are only exceptionally circular, being mainly elliptic, irregularly elongated into one or two directions. The epitheca becomes convex, while septa and dissepiments are introduced into the connecting processes (fig. 33). Moreover, lateral and syringoporoid buds arise, into which the prolongation of septa does not penetrate.

2. *Septal thickness variations.* Septa are the most plastic skeletal element of the studied species. Thin straight ones may occur in the same calyx with others elliptically inflated. Mature corallites have been measured with a micrometer, under 50 fold magnification, for thickness of septa, supplying the following numerical data:



Thickness of septa (in mm)	Number of septa (per cent)
0.1	16
0.2	23
0.3	28
0.4	20
0.5	18
0.6	4

The above figures show that septa 0.3 mm thick are the most common.

3. *Reduction of minor septa.* A tendency to the reduction of minor septa is a characteristic feature of this genus. The length of septa varies considerably, even within one corallite. Their rudimentary traces may be encountered with length one sixth to one eighth that of major septa. Others, however, are long, attaining three fourths of the length of major septa. Minor septa are often completely reduced. There may be one or two; in some calices, however, as many as 16.

4. *Dissepimental variation* is not markedly strong. Peneckielloid vesicles only occur, arranged into one, exceptionally two rows. The size of dissepiments varies, as is illustrated by numerical data representing the number of dissepiments in 2 mm:

Number of dissepiments	Number of corallites
3	1
4	8
5	11
6	9
7	5
8	1
9	1

Thus, extremely minute vesicles occur along with large ones. The predominant corallites, however, are those with large vesicles (5 dissepiments in 2 mm). The arrangement pattern of dissepiments varies too, usually vesicles rest horizontally, their vertical position is less common (fig. 31, 32).

5. *Spacing and structure of tabulae.* The arrangement of tabulae is not constant. Most frequently they are complete, flat, sometimes so regularly arranged as to give in longitudinal section the semblance of ladder steps, widely or closely spaced. In the same corallites, together with complete tabulae, the occurrence is noted of incomplete concave tabulae, consisting of strongly concave axial areas and of periaxial parts steeply inclined to the axial (fig. 31, 32).

## GENERAL CONSIDERATIONS

1. *Problems of colonial development*

In 1934 D. Hill pointed out the existence of several evolutionary trends in the phylogeny of some tetracoral lineages. One of them involves evolution from individual to colonial forms and, among the colonial group, from phaceloid and dendroid to massive forms. This concept finds its confirmation in the *Thamnophyllidae* where we can trace the evolution of the genus *Thamnophyllum*. In that lineage able of producing buds, which — after Alloiteau (1955, p. 396) — is the essential condition, the occurrence is noted of the three above mentioned colonial types: phaceloid in *Peneciella minor kunthi*, dendroid in *Sudetia lateseptata* and *Th. trigeminum kozłowskii*, and massive in the genus *Phillipsastraea*<sup>4</sup>. On the other hand, the genus *Macgeea* — throughout its phylogeny from the Lower Givetian to the Upper Frasnian — persists as an individual form. Very exceptionally only it produces 2-3 parricidal buds, although it occurs in the same facies with the dendroid *Thamnophyllum*. In the genus *Phillipsastraea*, the massive colonial stages have twice been attained by the *Thamnophyllum* lineage, i.e. in the Middle Givetian and the Upper Frasnian. Hence, we may assume that colonial development is not connected with facies or phylogeny, but with the adaptability of the given lineage.

A coral colony is an assemblage of corallites, more or less intimately united and produced by agamic multiplication (blastogeny) from one zooid. Hence it is a truly homogeneous population, consisting of genetically interrelated individuals. All the corallites of one colony are expected to display analogous reaction to outside stimulus, phenotypic variations of a continuous nature, and the occurrence of different mutations due to spontaneous changes in the genetic system.

Colonial corals have been recorded as early as from the Middle Ordovician (*Favistella*), up to recent times. A colony of Palaeozoic tetracorals, however, differs from a hexacoral one. In a tetracoral colony each corallite is separated from its neighbour by an epitheca. The epitheca is compact and stretches to the edge of the calyx, completely surrounding the polyp living there. It is formed during earliest ontogeny, as has been ascertained by the writer in representatives of *Disphyllidae*. In spite of this isolation of polyps in the colony, they must have been somehow connected by the soft tissues. This is indicated by the presence of a common holotheca covering the whole colony, and enclosing it as far as the calicinal edges, also by the constant shape of colonies in a fixed environment.

<sup>4</sup> After Schouppé (1958, p. 235) *Phillipsastraea hennahi* (Lonsd.) is provided with horse-shoe dissepiments, hence, the genus *Phillipsastraea* d'Orb. is an older synonym of the genus *Pachyphyllum* E. & H.

A hexacoral colony is markedly different. Polyps of one colony are closely interconnected, the epitheca is lacking, there is only a pseudotheca which may be synapticular, dissepimental (paratheca) or septal. Moreover, the operitheca is developed, characteristic of hexacorals.

Similar interconnection of corallites in one colony is observable in the family of Palaeozoic tetracorals, the Thamnophyllidae. Soshkina (1951) mentions them as displaying hexacoralloid character. Here also a pseudotheca only (septal or dissepimental) is formed to separate the corallites. In trioid colonies the wall separating the corallites arises from the septal bifurcation, while in plocoid colonies corallites are interconnected either by septa or by dissepiments. The wall is lacking here. During the ontogeny of Thamnophyllidae the bud does not produce an epitheca, but it is in intimate contact with the budding corallite, e.g. in the genera *Peneckiella* and *Adetia*, as well as in *Phillipsastraea*.

#### *Individual variation in colonial corallites*

a) *Ontogenetic changes of the bud.* A colony may be considered as a pure animal population. In them the palaeontologist can investigate the extent and intensity of variations, and at the same time study the evolutionary mechanism in chronologically different forms.

Every colonial corallite is subject to modification during blastogeny, analogously as the individual coral has to pass through certain ontogenetic stages. The morphological stages of development are usually uniform in buds of the same colony. E. g. every corallite of a massive colony of *Hexagonaria* begins its development within the dissepimentarium. Isolated by the epitheca it passes through the diaphragmatophoric and later — the pleonophoric stages. Finally, in mature individuals, laminar septa may become mesodaleoid. The ontogeny of the first corallite, i.e. the oozoid, from which the colony originates, has not been established. The development of the oozoid may differ from that of the blastozooid. For example, the oozoid of *Thamnophyllum trigeminum* Pen. passes the bilateral symmetry stage in early ontogeny, while no such stage is noted in buds. Populations of individual corallites have their own, specifically characteristic n/d ratio curve. The value of this ratio varies during ontogeny since the increase of the number of septa may be either allometrically negative or positive. In the same way colonial corallites display their own n/d or n/t ratio curves, and allometric intensity during blastogeny is likewise different.

Disphylloid and thamnophylloid buds may be distinguished already during ontogeny. Moreover, each of the four here considered genera displays peculiar blastogeny. In *Disphyllum* the bud, arising in the dissepimental part of the parent corallite, becomes disphylloidally lateral during further



evolution. In *Hexagonaria* it is disphylloidally intermural; in *Peneckiella* — thamnophylloidally lateral; in *Sudetia*<sup>5</sup> — two types of budding occur: thamnophylloidally lateral and syringoporoidal. Hence, on the basis of blastogeny, we may include each of these genera into higher systematic units and, moreover, secure a new diagnostic generic character. The presence within one genus of two types of blastogeny may, on the other hand, probably indicate generic divergence.

b) *Variability of mature colonial corallites.* The ontogeny of corallites in one colony is identical, but polymorphism of the mature corallites may be very strong. It displays a notable intensity range, depending on the phylogenetic stage of the given lineage, as well as on environment. This has been previously ascertained by the writer in colonial corallites and will be discussed here below.

*Disphyllum geinitzi*, which had probably lived in quiet deeper waters, is nearly stable. Slight variations only are noted in mature individuals. Corallite structure is not complicated. The particular skeletal elements are fully developed. No traces of reduction observable: septa laminar, without carinae and without peripheral regression. All this is suggestive of phylogenetic youth („phylojuvenile” forms). Colonial corallites are excellently adapted to the rather constant environmental conditions.

Modifications are unimportant and seemingly represent direct reaction against the internal environment factors within the colony, as well as those of external environment outside the colony. The internal environment factors probably reflect the „struggle” for space and food for the polyps. Corallites of a phaceloid colony, growing upward and having sufficient space available, are circular in section and only sporadically develop connecting processes (fig. 4). Closely spaced corallites touch each other by their walls and are irregular.

The dissepimentarium width, as compared with the tabularium, varies to a small extent. Rapid sedimentation is probably responsible for the appearance of larger dissepiments and more widely spaced complete tabulae.

*Hexagonaria laxa* displays a completely different variation range, as is also the case in its mutation *H. laxa jurkowicensis*. It seems that they represent two distinct ecological types within the studied reefs: a) *H. laxa* from Dziewki developed within a reef-facies, but, most likely, this part of the reef has not been exposed to the action of strong waves; b) the Jurkowice mutation, on the other hand, had probably lived on the surf-side of the reef.

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<sup>5</sup> In recent *Hexacoralla* a diagnostic feature may be one type of budding, though exceptions are noted too: in *Barabattoia mirabilis* Yabe & Sugiyama (1941, p. 72) together with intermural buds intracalicular are also encountered within one colony.

Adaptation of skeletal elements is expressed by thick septa (2-3 times thicker than those in *H. laxa*), massive trabecules (0.2 mm thick) and a massive wall.

Space available in the colony and easily gained food may have been decisive factors in differences of growth and budding of adjacent corallites. With the same number of septa (36-38) and diameter of tabularium (4.5—5.5 mm) some corallites have a broad dissepimentarium with large peripheral vesicles and they produce buds, while others are not capable of budding.

In mature corallites dissepimentarium width variations depend on the amount of space available and on budding. The size and spacing of vesicles may possibly be a function of external environment and rate of sedimentation, but it may also be associated with the budding process.

Development of septa which display every sign of degeneration, is a feature subject to strongest variations. Together with complete septa others occur in the same corallite, which are peripherally regressive and integrated into radiating segments. Carinate septa occur together with early smooth ones. The strong variability of reducing organs has been ascertained as early as in 1859 by Darwin. It was also confirmed by Simpson (1955). In the phylogerontic phase tetracorals vary strongly too.

Variability of mature corallites never exceeds here the limits of intraspecific variations. They are merely modifications within a population which is still genetically homogeneous. The individual colonial corallites may be arranged into a succession of continuous variation series, both in the above species and in *D. geinitzi*.

In recent colonial hexacorals, strong phenotypic variability is likewise encountered. Yabe & Sugiyama describe calicinal dimorphism and even polymorphism, as commonly reoccurring within the same colony of *Leptora columna* (1941, p. 75) and in *Astraeaopora tayama* (p. 84). Strong morphological variations have been also pointed out by Wells (1954) in *Stylopoenella armata* (Ehrenberg), *Acropora formosa* (Dana) and *A. polyorpha* Brook. They include shape of colony, depth and spacing of calices, length of septa and size of trabeculae. These variations are a function of water depth. The differences may be so great that fragments of two colonies may appear assignable to two distinct species if it were not for the occurrence of a number of forms linking the extreme variants.

*Peneckiella minor kunthi* — the colonies here are fasciculate, made up of straight, parallel corallites. In appearance they resemble *D. geinitzi* except that the particular corallites are thinner. Here, similarly as in *D. geinitzi*, short epithelial processes have developed to insure greater compactness of colonial structure.

Mature forms display notably strong variations expressed in every skeletal element. Two variation types are distinguishable: 1) somatic modifi-

cations reflecting the action of environment factors within the colony, and of environment factors outside the colony. These are slight quantitative changes varying in extent, but present in all corals. They constitute continuous variability involving thickness of septa, spacing of tabulae and dissepiments, also appearance of colony. The per cent variation curves of these characters are one-topped; 2) genetically conditioned variations expressed in the different phenotypes by qualitative changes suggestive of commencing divergence of features, leading perhaps to a new genus; here dissepiments and septa change structurally.

In our species dissepiments show strong diversity, since they may be horse-shoe like, peneckielloid, horizontal or sigmoidal. Such diversity is associated with regression of horse-shoe dissepiments. These may be small or large, numerous or completely lacking. Their extinction is accompanied by that of horizontal vesicles; sigmoidal dissepiments have originated from the fusion of horse-shoe like and horizontal dissepiments. The variability of the horse-shoe number/number of peneckielloid dissepiments is not continuous.

Septa are usually strongly thickened by a stereoplasm layer which surrounds the inner zigzag trabecular line. In some places the septa lose the superimposed stereoplasm layer thus revealing the carinae. Minor septa may vary in length so much so as to become rudimentary.

*Sudetia lateseptata* forms dendroid colonies. Minute, irregularly twisted individuals are closely intertwined and connected by extremely numerous connecting processes. Very strong variations are exhibited in the shape of the corallites. In cross section they may be circular, elliptic, or extremely irregular. Such variability is due to scarcity of space available within the colony, syringoporoid budding and numerous connecting processes.

In mature forms the particular skeletal elements are considerably thickened owing to the superimposition of stereoplasm, so much so that septa touch laterally. Corallites, as well as whole colonies thus augment their resistivity against the action of water. Dissepiments are large, tabulae very distant, indicating rapid reaction to accumulation of sediments.

The structure of dissepiments here differs from that in the ancestral species *Peneckiella minor kunthi*. The great diversity of shape has disappeared, the vesicles are all uniformly peneckielloid, differences are slight, quantitative.

Genetic changes are those of septal structure. Septa are here the disappearing element. This is expressed in the number of minor septa which are fully developed in some corallites, while in others several or nearly all will disappear. Similarly as in *P. minor kunthi*, a thick stereoplasm layer surrounds the inner zigzag trabecular line. On some septa trabecular



processes are set free through the reduction of stereoplasm. Septa are then provided with a new feature, i.e. with carinae which do not make their appearance before the maturity of forms. A new feature, which is not continuous, consists in syringoporoid budding.

### 3 Genomorphs

The appearance within *Peneckiella* and *Sudetia* colonies of new qualitative features together with others characterizing the genus *Thamnophyllum* which is their ancestral form, puts forward the problem of genomorphs so frequently discussed in literature. In 1905, Vaughan was the first to ascertain „diphyphylloid and lonsdaleoid modifications” in the genus *Lithostrotion*. In 1930, Lang and Smith (in Hill, 1934, p. 88) designated that phenomenon with the name of genomorphs. These authors have described the dimorphic genus *Lithostrotion* which, in the same colony, displays the structural pattern of the genus *Diphyphyllum* along with its own generic features. This new type in *Lithostrotion* colonies, corresponding to the genus *Diphyphyllum*, was by them called a genomorph. In the more recent papers by Dobroljubowa (1952, 1958), McLarren & Sutherland (1949), and Sutherland (1958) this problem is discussed at large.

Genomorphs are apparently recorded in greater abundance from Carboniferous coral colonies only. Smith (1945, p. 7) quotes the Devonian genus *Acelophyllum* as a genomorph within the species *Disphyllum caespitosum* (Goldf.). More recent papers have, however, revealed the clearly distinct microstructure of these two genera which makes them probably comparable to two suborders. Moreover, they never occur together in the same colony, hence they are not genomorphs.

Genomorphs occur in some corallites of both fasciculate and massive colonies, but the dimorphic structure scheme may likewise occur in one corallite.

At Mokrzyszów, in the Upper Frasnian *Peneckiella minor kunthi*, similarly as in *P. minor* (figured by Schouppé and in the thin slide of the second specimen), two structural patterns are observable, the thamnophylloid and the peneckielloid. In the same corallite horse-shoe dissepiments, accompanied by horizontal ones, may occur side by side with peneckielloid vesicles which are dominant.

*Peneckiella minor kunthi* is an objective subspecies, displaying its own characteristic curve of the growth  $n/d$  ratio and variable features ratio, both symmetrically in relation to the dominant mean (thickness of septa, major/minor septal length ratio). Together with the here dominating generic features of *Peneckiella*, the occurrence is noted also of receding thamnophylloid characters. The number of new dissepiments is on the average ten times that of the horse-shoe dissepiments. New qualitative features

diagnostic for genomorphs do not display typical continuity, but are distinctly predominant driving out the conservative features. These features are not associated with the age of the corallite, neither do they indicate maturity as do the lonsdaleoid septa of *Hexagonaria laxa*, but they appear in every ontogenetic stage of blastogeny. A peculiar feature is the early disappearance of horse-shoe dissepiments, while horizontal dissepiments still persist for some time, underlying the peneckielloid vesicles. Locally, the horizontal dissepiments disappear as well, and then the peneckielloid dissepiments are in direct contact with the wall. Thus *Peneckiella* loses this aspect of its hexacoral character.

*Peneckiella minor kunthi* occurs in the reef together with *Sudetia lateseptata*. Hence, colonies of these two species lived side by side and corallites of one genus coalesced frequently with those of the other one. In 24 thin slides *Sudetia* corallites are coalescent with those of *Peneckiella*.

*Sudetia lateseptata* now displays only few thamnophylloid features. Dissepiments are of uniform structure. The predominant syringoporoid buds occur together with a few only of those produced similarly as in *P. minor kunthi*. Outside of this, microstructure is thamnophylloid.

*Peneckiella minor kunthi* and *Sudetia lateseptata* are two species differing in their degree of adaptation to reef environment. They are very closely allied and linked by direct phyletic connections. They do not, however, represent species owing their formation to progressive divergence due to geographical isolation. The Mokrzyszów species must have developed through rapid evolution. They represent two stages of phylogenetic evolution: *Thamnophyllum* — *Peneckiella* and *Peneckiella* — *Sudetia*. As has already been ascertained by Sutherland (1958), evolution in the Carboniferous genus *Lithostrotion* is associated with neotenia. The simplified, regressive, terminal forms of *Sudetia lateseptata* must have been formed in this manner, too.

*P. minor kunthi* is very near to the phyletic end of the Thamnophylidae lineage. In this stage the morphological diversity of conspecific forms may be markedly strong. It does not, however, usually exceed intraspecific limits, as has been ascertained by the present writer in species of the Upper Frasnian genus *Phillipsastraea* (Rózkowska, 1953). In Mokrzyszów species, on the other hand, similarly as in the Carboniferous *Lithostrotion* forms, new qualitative features appear along with phenotypic variations, characteristic of the species *P. minor*. *Peneckiella*, in addition to thamnophylloid characters, realizes simplified dissepiments. *Sudetia* is already provided with peneckielloid dissepiments only and realizes a new, simple mode of budding along with the peneckielloid type. Aseptal buds in *Sudetia* resemble

the nepionic stage in *Protomacgeea dobruchnensis*, where the oozoidal pedicel is nearly aseptal too (Rózkowska, 1957).

*P. minor kunthi* is the synthetic form linking characters of the conservative lineage *Thamnophyllum* with the terminal form *Sudetia lateseptata*.

Among recent hexacorals, *Porites lichen* Dana (Wells, 1954, p. 453) displays marked variations of qualitative character. Corallites assignable to various species may occur within the same colony, since corallites provided with a columella may occur with others lacking the columella; the pali may be well developed or absent. In this connection Wells has ascertained the lack of a stabilized ecological form characteristic of the corresponding environment. *Porites lichen* may possibly be an example of a developing genomorph. We do not, however, know whether the new, rapidly developing qualitative characters, accompanied by simplified structure (atrophy of columella and pali) will predominate in the future and eliminate the ancestral characters giving rise to a new genus.

The following inferences may be drawn on the above observations of the Mokrzeszów forms.

a) The appearance of genomorphs is a real fact. Individuals with distinctly different structural scheme make their appearance among corallites of one colony displaying specific ancestral characters. The occurrence of new features takes place during various ontogenetic stages. In the first phase they still have to "struggle" for predominance with the preceding characters, e. g. peneckielloid dissepiments in *P. minor kunthi*.

b) The evolution of the colonial tetracorals, in which genomorphs occur, is orthogenetic since during the following stages conservative characters are completely eliminated by the new features, e.g. peneckielloid dissepiments in *Sudetia lateseptata*.

c) Phylogenetic development here progresses rapidly, as has been observed in the succession *Thamnophyllum* — *Peneckielia* — *Sudetia*. Two genera of *Peneckielia* and *Sudetia* are formed.

d) The appearance of genomorphs is associated with the phenomenon of simplification, since the new structural pattern is of regressive nature, the structure becomes simplified, as is shown in e.g. peneckielloid dissepiments, reducing minor septa and aseptal buds.

e) Genomorphs occur towards the close of the evolution of a lineage, as is the case in *Thamnophyllum* from the Upper Devonian.

f) Species of colonial tetracorals in which genomorphs occur may be of stratigraphic significance. Such is *Peneckielia minor*, widely spread in the Upper Frasnian (the Sudeten, Harz and Antitaurus Mountains), also *Sudetia*. The latter form has so far been recorded from the Upper Frasnian



of the Sudeten only. It is possible that some species, likewise provided with aseptal buds, and by Soshkina described as *Peneckiella*, are assignable here.

#### 4. Generic and specific diagnostic characters in Devonian colonial tetracorals

In connection with notable difficulties encountered in the identification of colonial tetracorals the writer will here try, perhaps still too early, to interpret some of her own observations. Different reasons may account for difficulties met during specific delimitation of colonial corals.

a) Phenotypic variability occurs in all the colonies, similarly as in the most homogeneous populations; its range may be very slight within one species, notably great in another. The extreme variants may then be regarded as distinct species.

b) Phylogenetic adaptation of various lineages to similar environmental conditions leads to convergency. It may be ascertained by detailed investigation of the ontogeny and microstructure, also of the structural scheme of a given lineage. The polyphyletic genus "*Hexagonaria*" is here an unquestionable illustration. It is an adaptative form, showing power of adaptation to the reef facies. The assignment of the genus "*Hexagonaria*" to various phyletic lines is confirmed by varying microstructure; i.e. trabecules may have a fan-like arrangement as in suborder Phillipsastraeacea Roemer (comp. Schouppé, 1958, p. 217), or be parallel as in the disphylloid group; dissepimental blastogeny may be of the thamnophylloid or disphylloid type, structure scheme disphylloid or stenophylloid.

Representatives of the genus *Hexagonaria* enter into various reef niches, hence they form various species and subspecies adapted to more limited ecological habitat. Specific characters here are adaptative and of a quantitative type. Every species exhibits variability in its own limits. In *Hexagonaria laxa* e.g. the maximum tabularium diameter is 6 mm, with 38 major and minor septa; while in *H. laxa jurkowicensis* this is 7 mm, with 40 septa. Similarly, septal thickness is limited too: in *H. laxa* — 17 per cent of corallites attain 0.4 mm, while in *H. laxa jurkowicensis* — 23 per cent of the corallites in one colony attain the figure of 1.3 mm.

In tetracorals, species are established on morphological characters, structure of septa, mode of budding, and on correlations such as the n/d allometry growth curve, length ratio of major septa to that of the minor, septal length range, the dissepimentarium/tabularium width ratio. Since variability of morphological characters occurs everywhere and is of continuous nature, species is characterized by one-topped biometric curves of the various features.

A species differs from a subspecies in features of quantitative nature only. Hence the n/d or n/t allometry line has the same style, being only slightly displaced into the direction of that character which is allometrically predominant. E.g. the difference between *H. laxa* and *H. laxa jurkowicensis* is indicated by the allometrically positive increase of the number of septa during phylogeny. Biometrical curves partly coincide, e.g. that of the tabularium/dissepimentarium variability ratio.

*Thamnophyllum trigeminum* Pen.<sup>6</sup> (= *Th. trigemme* (Quenst.)) (in Rózkowska, 1957), is a good illustration of the intraspecific variability and value of the above quoted criteria. This is a conservative species, which has persisted in the Devonian of Poland from the Givetian through the Frasnian. Throughout that period it retains the same structural pattern, analogous ontogeny, parricidal blastogeny, and the same type of allometry. It may, however, be separated into several varieties which, in 1956 and 1957, were by Rózkowska incorrectly assigned to distinct species. Their biometrical curves partly coincide, unless they are separated by the incompleteness of material or a sedimentary gap. All these „species” may be reasonably considered as subspecies of *Thamnophyllum trigeminum* Pen. Hence, upwards from the Lower Givetian to the Frasnian the following mutations will be encountered within *Thamnophyllum trigeminum*: *Th. trigeminum* Pen., *Th. skalense* Rozk., *Th. trigeminum trigeminum* Pen., *Th. trigeminum* Pen. *ajchela* Rozk., *Th. trigeminum* Pen. *kozłowskii* Rozk. and *Th. trigeminum* Pen. *superius* Rozk.

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<sup>6</sup> H. Flügel (1959, p. 117) has proved the priority of the specific name *Thamnophyllum trigeminum* Penecke in respect to the name *Th. trigemme* Pen. The species *trigemme* Quenstedt has by Flügel been included into the genus *Favistella* Dana.

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MARIA RÓŻKOWSKA

BLASTOGENEZA I ZMIENNOŚĆ OSOBNICZA W KOLONIACH TETRACORALLA  
Z DEWONU POLSKI

## Streszczenie

W pracy opisana została morfologia, blastogeneza oraz zmienność osobnicza wewnątrzkolonijna u pięciu przedstawicieli *Tetracoralla* z dewonu Gór Świętokrzyskich i Sudetów. Materiał ten pozwolił poczynić ogólne obserwacje, dotyczące zagadnienia kolonijności, procesu blastogenezy, zmienności osobniczej w kolonii oraz cech diagnostycznych gatunkowych i rodzajowych.

Istnieją grupy koralu nie przejawiających zdolności pączkowania, obok innych, mających te zdolności. Do tych ostatnich należą *Thamnophyllidae* z rodzajami *Peneckiella*, *Sudetia* i *Phillipsastraea*. Kolonie ich, żyjące równocześnie, są faceloidalne, krzaczaste i masywne. Pokrój kolonii jest funkcją środowiska, a nie stadium filogenetycznego danego szczepu. Kolonie u *Hexacoralla* są bardziej progresywne, niż u *Tetracoralla*. U *Tetracoralla* osobniki oddzielone są epiteką i zachowują silną indywidualność; u *Hexacoralla* zmniejsza się indywidualność osobników, gdyż łączy je wspólna pseudoteka i pojawia się peryteka. Wśród *Tetracoralla* tylko rodzina *Thamnophyllidae* (Soshkina, 1951) przejawia charakter heksakoraloidalny, gdyż brak tu epiteki, osobniki zaś połączone są pseudoteką.

Ontogeneza oozoida jest u form kolonijnych mało znana. Przechodzi on przez stadium symetrii bilateralnej. Blastogeneza jest mniej prawidłowa. Początek wszystkich pączków jest intrakalicynalny. Dalszy jego rozwój jest różny u zbadanych tutaj rodzajów. Wśród nich wyróżnić można dwa typy pączkowania, zależnie od wytwarzania epiteki między pączkiem a koralitem pączkującym: typ dysfoidalny i typ tamnofyoidalny. Rozwój pączka może się odbywać w kolonii cerioidalnej między ścianami (pączki intermuralne), jak u *Hexagonaria laxa*, lub może wyjść poza kielich osobnika macierzystego, odchylając się odeń, zabierając jednak część jego septów, które się zachowują po stronie zewnętrznej pączka. Jest to pączkowanie lateralne, jak u *Disphyllum geinitzi*. U form tamnofyoidalnych pączek lateralny zachowuje septa kielicha pączkującego po swojej stronie zewnętrznej i przyosiowej (*Peneckiella minor kunthi*). Przy pączkowaniu syringoporoidalnym (*Sudetia latiseptata*) pączek rozwija się jako wyrostek boczny, nie mający w ogóle septów w fazie najmłodszej.

Zmienność osobnicza w obrębie kolonii jest bardzo różnorodna: najmniejsza u form filojuwenilnych, u których istnieją struktury filogenetyczne młode, a najbardziej urozmaicona u filogerontycznych, u których pewne elementy ulegają atrofii. Zmienność morfologiczna jest także nie tylko funkcją stadium filogenetycznego, lecz również środowiska. Polimorfizm bowiem jest niewielki w facji głębszego, cichego morza, natomiast znaczny w facji rafowej.

Pojęcie genomorfu wprowadzone zostało przez Langa i Smitha (1930) dla dymorficznego rodzaju *Lithostrotion*, który w tej samej kolonii, obok osobników o bu-

owe charakterystycznej dla *Lithostrotion*, zawiera inne, o budowie takiej, jak *Diphyphyllum*. *Diphyphyllum* jest tutaj genomorfem. Genomorfy rozpowszechnione u form karbońskich; szerzej zostały opisane przez Sutherlanda (1958) i Dobrolubową (1949, 1958). Genomorfy występują w *Peneckiella minor kunthi*, gdzie obok planu budowy *Thamnophyllum* (dissepimenta horyzontalne i podkowiaste oraz wachlarze abekul) zaznacza się nowa cecha, jaką stanowią dissepimenta penekielloidalne; wy-erają one dissepimenta tamnofyloidalne, przewyższając je liczbowo aż siedmio-otnie. Obie struktury występują w jednym koralicy w różnych stadiach blasto-ney. U *Sudetia lateseptata* występują już tylko pęcherze penekielloidalne, lecz po-ia się nowy typ pączkowania intrakalicynalnego: syringoporoidalne pączki ase-ine; natomiast blastogeneza taka, jak u *Peneckiella*, występuje już tylko spora-ienie. Oba gatunki żyjące tuż obok siebie spokrewnione są bezpośrednio i powstały epewne w drodze szybkiej ewolucji; odpowiadają one dwu etapom rozwoju filoge-tycznego: od *Thamnophyllum* do *Peneckiella* i od *Peneckiella* do *Sudetia*.

Rozwój i powstawanie genomorfów połączone jest prawdopodobnie ze zjawiskiem otentii (Sutherland, 1958). Genomorfy są to uproszczone formy regresywne, poja-ające się przy końcu rozwoju szczepu, jak np. *Peneckiella* i *Sudetia* przy końcu olucji szczepu *Thamnophyllum*.

Wielkie trudności wyłaniają się przy oznaczaniu gatunkowym form kolonij- ch z następujących przyczyn: 1) amplituda zmienności jest różna, zwłaszcza duża form filogerontycznych, a więc warianty krańcowe można mylnie uważać za od- ielne gatunki; 2) zjawisko konwergencji występuje często u gatunków kolonijnych est powodem, że gatunki należące do różnych szczepów filogenetycznych bywają ącane do jednego rodzaju. Klasycznym przykładem jest polifiletyczny rodzaj *Tragonaria*. Przy oznaczaniu gatunku należy uwzględnić cechy morfologiczne osob- ków dojrzałych i rozwój ontogenetyczny szeregu skorelowanych cech. Ważne jest zbadanie zmienności fenotypowej, gdyż dla gatunku charakterystyczne są jed- wierzchołkowe krzywe biometryczne. Podgatunek ma taki sam co gatunek plan dowy, jednakową mikrostrukturę i blastogenezę. Różnice ilościowe występują przesunięciach linii allometrycznych oraz w krzywych biometrycznych, pokrywa- ych się częściowo z krzywymi osobników typowych. Przykładem tego jest *Tham- phyllum trigeminum* Penecke, występujący w Polsce od żywetu do górnego franu worzący w tym czasie 5 podgatunków. Cechy diagnostyczne rodzaju są jakościowo rdziej uogólnione, zaś jego zasięg geograficzny duży. Obok cech charakteryzują- ch rodzinę, do której należy, ma on zarówno swoistą ontogenezę oozoidu, jak i bla- genezę oraz właściwy sobie pokrój kolonii.

Zagadnienia te zbadane zostały na podstawie przeprowadzonej analizy morfo- icznej 4 gatunków i 1 podgatunku, które scharakteryzować można jak następuje.

*Disphyllum geinitzi* L. & S. (fig. 2-8), z Sitkówki k. Kielc (żyweckie wapienie g-niczne), tworzy kolonie faceloidalne. Blastogeneza jest na początku intrakali- na, jak u wszystkich Tetracoralla. Pączek już wcześniej w ontogenezie oddziela



się epiteką od koralita macierzystego. Gatunek ten ma budowę prostą, bez śladów uwstecznienia. Żył on zapewne w nieco głębszym morzu. Zmienność osobnicza jest niewielka; przejawia się tylko w umieszczeniu tabul, w wielkości dissepimentów, w proporcji długości septów I i II rzędu oraz w grubości septów.

*Hexagonaria laxa* Gürich (fig. 9-16), z Dziewek k. Siewierza (żyweckie rafy stromatoporoidowo-tabulatowe), tworzy kolonie cerioidalne, przy czym poszczególne osobniki oddzielone są od siebie zwartą epiteką. Zmienność morfologiczna jest bardzo duża, gdyż forma ta znajduje się w stadium filogerontycznym i rozwijała się w środowisku niespokojnym, rafowym. Pączek pojawia się w narożach o silnie uwsteczniionych septach lonsdaloidalnych, gdzie istnieją ponadto duże, lecz rzadkie dissepimenta. Już wczesnie pączek oddziela się od osobnika macierzystego epiteką, otoczoną po obu stronach pseudoteką. Przyrost liczby septów jest allometrycznie ujemny. Zmienność osobnicza przejawia się też w stosunku tabularium do dissepimentarium i w gęstości tabul i dissepimentów (jako reakcja na szybkość sedymentacji). Największą zmienność wykazują septa: zmienny jest stosunek długości septów I rzędu do II-go, ich grubość, liczba listewek, ich stopień rozpadu na kolce. Potwierdza się tu obserwacja Darwina (1859) i później Simpsona (1955), według której największa skala zmienności występuje w redukujących się organach.

*Hexagonaria laxa jurkowicensis* n. subsp. (fig. 17-19), z Jurkowic pod Opatowem (górnio-żywecka rafa stromatoporoidowo-tabulatowa), tworzy kolonie cerioidalne. Ten nowy podgatunek różni się od formy typowej nieco większymi rozmiarami kielichów ( $16 \times 18$  mm), tabulariów (7 mm), większą liczbą septów (do 20-tu I rzędu) i dalej posuniętą atrofią septów. Septa II rzędu są nieco dłuższe, niż u formy typowej. Blastogeneza — jak u gatunku *H. laxa*, z tą różnicą, że pączki wyrastają promieniście z kielicha. Współczynnik  $n/d$  ma większą wartość, niż u formy z Dziewek, gdyż liczba septów jest większa, wobec czego linia allometrii jest nieco przesunięta w porównaniu z linią tą u formy typowej. Polimorfizm osobników jest bardzo duży, podobnie jak u formy typowej, lecz septa nie rozpadają się na kolce, ale na poprzeczne bryłki. Mikrostruktura septów jest dysfyloidalna. Trabekule grube (0,2 mm). Elementy strukturalne grube, o dużej zmienności. Forma ta rozwijała się w strefie kipieli.

*Peneckiella minor* (Roemer) *kunthi* (Dames) (fig. 20-29), z Mokrzeszowa, D. Śląsk (górnio-frańska rafa koralowa), tworzy kolonie faceloidalne. Blastogeneza jest tamno-fyloidalna, tzn. pączek nie oddziela się od osobnika macierzystego epiteką, lecz łączy się z nim pseudoteką. Grube trabekule septalne (0,16 mm) tworzą niesymetryczne wachlarze. Przyrost septów podczas ontogenezy jest allometrycznie dodatni, w stadium efebicznym — ujemny. Polimorfizm jest bardzo duży, przejawiając się zwłaszcza w septach, które i tutaj ulegają uwsteczniению. Poza tym ustępują charakterystyczne dla *Thamnophyllum* dissepimenta horyzontalne i podkowiaste, wypierane przez nowe, bardzo proste dissepimenta penekielloidalne. Od formy z Grund, której amplituda zmienności nie jest znana, odmiana z Mokrzeszowa różni się większą liczbą septów.

*Sudetia lateseptata* n. gen., n. sp. (fig. 30-33, szlify mikroskopowe nr 12 i 15), Mokrzeszowa, D. Śląsk.

Diagnoza holotypu: kolonia krzaczasta, o nieregularnie powyginanych koralikach, mających — przy średnicy 3,0-4,6 mm — 32-36 septów I i II rzędu. Gruba epiteka; pograniczu dissepimentarium i tabularium — pseudoteka wewnętrzna. Kielich głęboki, o płaskim dnie i stromych ścianach. Septa I rzędu krótkie, szerokie, z listewkami zasłoniętymi przeważnie stereoplazmą; septa II rzędu na ogół uwstecznione. Jeden szereg dissepimentów penekielloidalnych; tabule przeważnie komórkowe, wklęsłe; niesymetryczne wachlarze trabekul; beleczki grubości 0,06-0,18 mm. Rozmnożanie dwojaki: rzadziej lateralne, tamnofyloidalne, często syringoporoidalne, najwcześniejszych zaś stadiach — aseptalne (fig. 30-43).

Gatunek ten występuje w rafie wespół z *P. minor kunthi*. Osobniki obu form przrastają do siebie. Krzaczaste kolonie i elementy szkieletowe silnie pogrubiałe zwierciadlają przystosowanie do życia w rafie. Pączki są dwojakie: lateralne, tamnofyloidalne — jak u *P. minor kunthi* oraz syringoporoidalne. Mają one budowę cystifyloidalną i są aseptalne. Po stadium aseptalnym następuje stadium brewisepialne, kiedy pojawiają się septa krótkie, cienkie. U form dojrzałych septa są grube i do zetknięcia się, septa zaś II rzędu wypadają prawie wszystkie. Podobne pączki aseptalne z budową cystifyloidalną opisała Soshkina (1955) u *Peneckiella jevlanensis* Ilvanker. Polimorfizm jest bardzo duży, widoczny w pokroju koralitów i budowie septów. Nowe dissepimenta penekielloidalne są natomiast bardzo jednolite. Przyrost liczby septów n/d i stosunek średnicy wolnej od septów przestrzeni osiowej (c) do średnicy koralita — są podobne jak u *P. minor kunthi*. Uwidocznione to jest na fig. 43.

#### OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 5)

Mapa rozmieszczenia miejscowości, z których pochodzą zbadane formy.

Fig. 2 (p. 8)

*Disphyllum geinitzi* Lang & Smith; Sitkówka, żywet. Przekrój poprzeczny koralika.

Fig. 3 (p. 8)

*Disphyllum geinitzi* Lang & Smith; Sitkówka, żywet. Przekrój podłużny młodego osobnika, oddzielonego od macierzystego częściowo już powstałą nową epiteką (e).

Fig. 4 (p. 9)

*Disphyllum geinitzi* Lang & Smith; Sitkówka, żywet. Poprzeczny przekrój pączka stadium nepionicznego; zaczątki nowej epiteki (e) i pseudoteki (p).

Fig. 5 (p. 10)

*Disphyllum geinitzi* Lang & Smith; Sitkówka, żywet. Przekrój poprzeczny pączka stadium późnonepionicznym; epiteka i nowe septa częściowo utworzone.

Fig. 6 (p. 10)

*Disphyllum geinitzi* Lang & Smith; Sitkówka, żywet. Przekrój poprzeczny sta-

dium wczesnoneanicznego; nowa epiteka prawie utworzona pomiędzy dwiema pseudotekami ( $p_1$ ,  $p_2$ ) u trzech osobników, ściśle ze sobą połączonych przez pączkowanie.

Fig. 7 (p. 11)

*Disphyllum geinitzi* Lang & Smith; Sitkówka, żywet. Przekrój podłużny pączka z epiteką (e), oddzielającą go w stadium neanicznym od koralita macierzystego.

Fig. 8 (p. 12)

*Disphyllum geinitzi* Lang & Smith; Sitkówka, żywet. Krzywa korelacji n/d; na osi odciętych — średnice koralitów (d), na osi rzędnych — liczba septów I rzędu (n).

Fig. 9 (p. 14)

*Hexagonaria laxa* Gürich; Dziewki, żywet. Przekrój poprzeczny kolonii cerioidalnej.

Fig. 10 (p. 14)

*Hexagonaria laxa* Gürich; Dziewki, żywet. Przekrój podłużny kolonii cerioidalnej.

Fig. 11 (p. 15)

*Hexagonaria laxa* Gürich; Dziewki, żywet. Przekrój poprzeczny koralita, przystawiającego miejsce na dwa pączki (1, 2).

Fig. 12 (p. 15)

*Hexagonaria laxa* Gürich; Dziewki, żywet. Przekrój poprzeczny pączka w stadium nepionicznym; e nowa epiteka pączka.

Fig. 13 (p. 16)

*Hexagonaria laxa* Gürich; Dziewki, żywet. Przekrój poprzeczny pączka (b) w stadium późnonepionicznym; epiteka jeszcze niecałkowita.

Fig. 14 (p. 16)

*Hexagonaria laxa* Gürich; Dziewki, żywet. Przekrój poprzeczny pączka w stadium neanicznym.

Fig. 15 (p. 18)

Krzywa korelacji n/t; na osi odciętych — średnice tabulariów (t), na osi rzędnych — liczba septów I i II rzędu (n). Linia przerywana i kropki — dane dla *Hexagonaria laxa* Gürich (Dziewki, żywet); linia ciągła — *H. laxa jurkowicensis* Rózk. (Jurkowice, żywet).

Fig. 16 (p. 19)

Krzywa korelacji t/diss; na osi odciętych — stosunek średnicy tabularium (t) do szerokości dissepimentarium (diss), na osi rzędnych — % osobników. Linia przerywana — *Hexagonaria laxa* Gürich (Dziewki, żywet); linia ciągła — *H. laxa jurkowicensis* Rózk. (Jurkowice, żywet).

Fig. 17 (p. 24)

*Hexagonaria laxa jurkowicensis* Rózk.; Jurkowice, żywet. Przekrój poprzeczny kolonii cerioidalnej.

Fig. 18 (p. 24)

*Hexagonaria laxa jurkowicensis* Rózk.; Jurkowice, żywet. Przekrój podłużny kolonii cerioidalnej.

Fig. 19 (p. 24)

*Hexagonaria laxa jurkowicensis* Rózk.; Jurkowice, żywet. Przekrój poprzeczny części koralita z pączkiem w stadium nepionicznym; brak jeszcze nowej epiteki.



Fig. 20 (p. 29)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekroje poprzeczne dojrzałych koralitów: A koralit przyrasta wydłużoną częścią brzeżną do sąsiada, B pęczek w połączeniu z koralitem macierzystym.

Fig. 21 (p. 30)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój poprzeczny koralita z wyraźnymi listewkami na septach, często niezasłoniętymi stereoplazmą.

Fig. 22 (p. 30)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój podłużny koralita.

Fig. 23 (p. 30)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój poprzeczny koralita z pączkiem; septa koralita macierzystego wydłużając się wchodzi w pączek.

Fig. 24 (p. 31)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój pączka mającego już całkowitą pseudotekę.

Fig. 25 (p. 31)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój podłużny pączka; brak epiteki między obu osobnikami.

Fig. 26 (p. 32)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Krzywa korelacji między liczbą septów ( $n$ ) i średnicą koralitów ( $d$ ), oraz szerokości pola osiowego ( $c$ ) od septów i średnicą koralitów ( $d$ );  $c$ ,  $d$  — w mm.

Fig. 27 (p. 33)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój podłużny: widoczne podkówki, pęcherze penekielloidalne, horyzontalne i sigmoidalne; wachlarze bekularne oparte na podkówkach lub na normalnych (penekielloidalnych) pęcherzach.

Fig. 28 (p. 33)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój podłużny przedstawiający różne dissepimenta.

Fig. 29 (p. 35)

*Peneckiella minor kunthi* (Dames); Mokrzeszów, górny fran. Przekrój podłużny przedstawiający różnorodne dissepimenta oraz gęste, poziome tabule.

Fig. 30 (p. 35)

*Sudetia lateseptata* Rózk.; Mokrzeszów, górny fran. Przekrój poprzeczny koralita; septa II rzędu prawie zupełnie zredukowane.

Fig. 31 (p. 36)

*Sudetia lateseptata* Rózk.; Mokrzeszów, górny fran. Przekrój podłużny.

Fig. 32 (p. 36)

*Sudetia lateseptata* Rózk.; Mokrzeszów, górny fran. Przekrój podłużny.

Fig. 33 (p. 37)

*Sudetia lateseptata* Rózk.; Mokrzeszów, górny fran. Przekrój podłużny przedstawiający pokrój osobnika z pączkiem syringoporoidalnym (A) i wyrostkiem czepnym (B).

Fig. 34 (p. 38)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Przekrój poprzeczny osobnika wraz z pączkiem aseptalnym.

Fig. 35 (p. 38)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Przekrój poprzeczny pączkującego koralita wraz z nieco ukośnie przekrojonym pączkiem aseptalnym.

Fig. 36 (p. 38)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Pączek z trzema septami, przylegający do koralita sąsiedniego; oba w przekroju poprzecznym.

Fig. 37 (p. 38)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Pączek nieco dalej rozwinięty, stadium brewiseptalne z wyrostkiem czepnym.

Fig. 38 (p. 39)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Młody osobnik w stadium neanicznym, przylegający do koralita sąsiedniego.

Fig. 39 (p. 39)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Osobnik pączkujący, wraz z pączkiem, w przekroju podłużnym nieco ukośnym.

Fig. 40 (p. 39)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Pączkowanie tamnofylloidalne, wydłużone septa koralita pączkującego wchodzi do pączka.

Fig. 41 (p. 40)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Młodociany osobnik, prawdopodobnie oozoid, mający u samej już podstawy septa od najwcześniejszego stadium.

Fig. 42 (p. 40)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Młodociany osobnik, prawdopodobnie oozoid, w przekroju podłużnym nieco ukośnym, z pączkiem cystifyloidalnym na końcu dystalnym.

Fig. 43 (p. 41)

*Sudetia lateseptata* Róžk.; Mokrzyszów, górny fran. Krzywa korelacji łącznej liczby septów ( $n$ ) i średnicy koralitów ( $d$ ), oraz szerokości pola osiowego wolnego od septów ( $c$ ) i średnicy koralitów ( $d$ );  $c$ ,  $d$  — w mm.

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МАРИЯ РУЖКОВСКА

## БЛАСТОГЕНЕЗ И ИЗМЕНЧИВОСТЬ ОСОБЕЙ В КОЛОНИЯХ ЧЕТЫРЕХЛУЧЕВЫХ КОРАЛЛОВ ИЗ ДЕВОНА ПОЛЬШИ

### Резюме

В настоящей работе описано морфологию, бластогенез и изменчивость особей в колониях пяти представителей четырехлучевых кораллов из девона Свентокржиских Гор и Судетов. Этот материал дал возможность произвести

наблюдения касающиеся в особенности колониальности, изменений происходящих в бластогенезе и явления геноморфов.

В колониях *Disphyllum geinitzi* и *Hexagonaria laxa jurkowicensis*, как и у всех четырехлучевых кораллов, сильно подчеркнута индивидуальность отдельных особей, вполне отделенных друг от друга эпитекой. Вместо того у *Sudetia lateseptata* и *Peneckiella minor kunthi* преобладает индивидуальность колонии, потому что, будучи представителями гексакораллоидных *Thamnophyllidae*, имеют особи соединенные ложными стенками.

Изменения в бластогенезе сочетаются с формой колонии и ввиду этого являются функцией среды. Каждый род обладает собственным типом почкования, а в случае когда выступают два разных типа, так они связаны с явлением филетической дивергенции.

Автор обсуждает вопрос геноморфов. Понятие это введено Лангом и Смисом (Lang & Smith, 1930) для диморфного рода *Lithostrotion*, который в одной и той же колонии, рядом с особями со строением характерным для *Lithostrotion*, содержит особи обнаруживающие строение свойственное *Diphyphyllum*. *Diphyphyllum* является тут геноморфом. Геноморфы распространены среди карбонских форм; более широко описаны Сасерлендом (Sutherland, 1958) и Добролюбовой (1949, 1958).

Явление геноморфов проявляется в материале автора у *Peneckiella minor kunthi*, у которой наряду с тамнофиллоидной структурой (веера трабекул, горизонтальные и подковообразные диссепименты) встречается пенекиеллоидная структура (пенекиеллоидные диссепименты), а также у *Sudetia lateseptata*, у которой, рядом с тамнофиллоидной структурой (веера трабекул, боковое почкование как у *Peneckiella*), имеются цельные пенекиеллоидные диссепименты и сырингопородные почки. Оба эти вида представляют две стадии быстрого развития от *Thamnophyllum* до *Peneckiella* и от *Peneckiella* до *Sudetia*.

Эти вопросы были исследованы на основании проведенного морфологического анализа 4 видов и 1 подвида, которые можно охарактеризовать следующим образом.

*Disphyllum geinitzi* Lang & Smith (фиг. 2-8) из Ситковки около Кельц (верхний живет), с фацеллоидными колониями, образует боковые почки, берущие свое начало в диссепиментариуме. Почки быстро отделяются посредством эпитеки, на которой возникают новые перегородки для обеих особей — материнского кораллита и почки; между тем часть перегородок почкующей особи сохраняется в почке на ее наружной стороне. Вид этот является филогенетической формой живущей в спокойном море, что отражается в малой амплитуде морфологической изменчивости. Модификация в строении перегородок, устоте дний и величине диссепиментов, являются тут функцией внешней среды.

*Hexagonaria laxa* Gürich (фиг. 9-16) из Дзевок около Севержа (средний живет) и его мутация *H. laxa jurkowicensis* n. subsp. из Юрковиц около Опа-



това (верхний живет), из рифовой фации с цериоидными колониями. Почки развиваются тут целиком в пределах диссепиментариума и рано отделяются эпитекой. Обе формы находятся на высоком уровне филогенетического развития, что проявляется в лондалоидном строении перегородок и в присутствии планочек. С явлением редукций связан широкий диапазон изменчивости в строении перегородок, а влияние подвижной морской среды становится видным по толщине элементов скелета и расположении дниц и диссепиментов.

Подвид *H. laxa jurkowicensis* (фиг. 17-19) отличается от типичной формы большим диаметром чашечки (16 × 18 мм), табуляриумов (7 мм), большим количеством перегородок (до 20-ти, I цикла) и более сильной атрофией перегородок. Перегородки II цикла несколько длиннее чем у типичной формы.

*Peneckiella minor* (Roemer) *kunthi* (Dames), (фиг. 20-29), из Мокржешова (Судеты, верхний фран), из кораллового рифа, с фацеллоидными колониями. Почкование тамнофиллоидное, т. е. почка не отделяется эпитекой от почкующего кораллита. Часть его перегородок входит в состав приосевой части чашечки почки. Большая амплитуда изменчивости проявляется в строении диссепиментов, так как горизонтальные и подковообразные диссепименты бывают вытеснены характерными для этого рода пенекиеллоидными. Большая изменчивость видна также в строении перегородок, их толщине и появлении септальных планок. Наряду с такими генетическими изменениями реакция на внешние импульсы проявляется в расположении дниц и величине пузырей.

*Sudetia lataseptata* n. gen., n. sp. (фиг. 30-43); микроскопические шлифы № 12 и 15). Диагноз голотипа: колония кустистая с неправильно изогнутыми кораллитами, обладающими при диаметре 3,0—4,6 мм от 32 до 36 перегородок I и II цикла. Под эпитекой толстая ложная стенка на границе между табуляриумом и диссепиментариумом. Чашечка глубокая, с плоским дном и отвесными стенками. Перегородки I цикла короткие, широкие, с планками прикрытыми по большей части стереоплазмой; перегородки II цикла часто полностью редуцированы; один ряд пенекиеллоидных диссепиментов; дница преимущественно полные, вогнуты; несимметрические веера трабекул (трабекулы толщиной 0,06—0,18 мм). Почкование двоякого рода: реже боковое как у *Peneckiella*, чаще сырингопоройдное, а на наиболее ранних стадиях — асептальное.

Форма эта жила рядом с *P. minor kunthi* и зачастую прирастала к ее кораллитам. Рядом со спорадическими боковыми почками, как у *P. minor kunthi*, распространено почкование сырингопоройдное. Тут можно выделить две более молодые стадии: асептальную (констатированную у *Peneckiella jevlenensis* Bulv. Сошкиной, 1954) и бревисептальную. Генотиповая изменчивость проявляется в строении перегородок, которые подвергаются атрофии, а влияние среды видно из расположения дниц и диссепиментов равно как и в общей форме нерегулярных кораллитов кустистой колонии.

JULIAN KULCZYCKI

POROLEPIS (CROSSOPTERYGII) FROM THE LOWER DEVONIAN  
OF THE HOLY CROSS MOUNTAINS

*Abstract.* — On the basis of the here described remains a new interpretation is given of the structure of the anterior part of the head in *Porolepis*. The writer postulates also the lack of direct relationship between holoptychioids (*Porolepiformes*) and tetrapods.

INTRODUCTION

The results are here reported of research work on the fossil remains of *Porolepis* from the Lower Devonian of the Holy Cross Mountains (Góry Świętokrzyskie).

The studied material was collected during the 1956 summer season at Daleszyce, 15 km east of Kielce. It consists of imprints of fish remains preserved in quartzitic sandstone. All the specimens represent negatives formed owing to the leaching of skeletal elements by solutions migrating through the rock after its consolidation. Though bony tissue has not been preserved, the here discussed imprints and casts reveal an astonishing number of minute structural details. It is often possible to distinguish even the boundary between parts previously occupied by cartilage and membraneous bones. Data have likewise been obtained in respect to the shape of various cavities and the position of most openings, nerve and vessel canals, though, naturally, their complete course cannot usually be traced. Lack of deformation in most specimens is another favourable circumstance. Their excellent and unbiased preparation, effected by nature herself, excludes the risk of the formation of artefacts during the preparation of the material. It is often difficult to avoid them, particularly so when differences between the tissue and the rock material in respect to colouration, hardness, etc., are hardly discernible.

The preparation of material consisted in the first place in the removal of the silt, filling cavities which represents casts of bone remains. The cleaning

was often a difficult task owing to the risk of damaging the minute canal casts. Since the studied specimens are in the form of cavities, with wall surfaces often invisible, the next stage of work consisted in the preparation of latex casts.

All these technical tasks, as well as the preparation of the paper, have been carried out at the Palaeozoological Department of the State Natural History Museum in Stockholm where the author could spend six months thanks to a grant from the Polish Academy of Sciences.

The most sincere thanks are here conveyed by the writer to Professor E. A. Stensiö and to his collaborators Professor E. Jarvik and Dr T. Ørvig, for their hospitality, the facilities offered for research work, the access to all the required technical equipment and comparative materials. Through their great courtesy, the writer was permitted the access to unpublished manuscripts of papers on placoderms, on the lepidomorial and the delamination theory, and provided with all the necessary explanations.

Before commencing his work in Stockholm the writer had the opportunity to visit a number of other European centres of palaeoichthyological studies and to inspect the faunal collections there. He now desires to make his acknowledgement of the courtesy and assistance rendered by Professor A. Heintz of Oslo, Professor J. P. Lehman of Paris, Dr Lector E. Nielsen and Dr H. Bjerring of Copenhagen, Professor D.M.S. Watson and Professor E. I. White of London.

The warmest thanks are due to Professor R. Kozłowski, Head of the Palaeozoological Institute of the Polish Academy of Sciences in Warsaw. It is his friendly help that enabled the writer not only to collect the here described material, but also to carry out the required amount of research work abroad.

During the preparation of specimens and latex casts Miss A. Brash of the Palaeozoological Department of the State Natural History Museum in Stockholm offered kind help and valuable suggestions. Mr U. Samuelson of the same Department made some of the plate photographs. Others were made by Miss M. Czarnocka of the Palaeozoological Laboratory of the Polish Academy of Sciences in Warsaw. Mrs J. Humnicka has translated the paper into English.

The writer wishes to express to them all his most sincere thanks.

\*

The terminology used in this work is chiefly that of E. Jarvik (1942). New terms have been introduced: 1° in the lack of a Latin equivalent of the existing English term, Jarvik's „olfactory ridge" has been replaced by „eminentia olfactoria"; 2° in view of some important difference of interpretation, due to which the heretofore accepted term would contradict the nature of



the given morphological element, or when a term was previously reserved for another non-homologous anatomic element (e.g. „crista rostro-caudalis” is replaced by „crista subnarina” with reference to the crest in the nasal cavity of *Porolepis*); 3° in the lack of a term for the described element.

## DESCRIPTIVE PART

### *Porolepis ex grege posnaniensis* (Kade, 1858)

*Material.* — Negatives of 5 fragments of the ethmoidal region, two with preserved orbital region; 1 basisphenoid; 6 fragments of the lower jaw; a number of detached teeth and scales, also fragments most probably representing the shoulder girdle and the gular bone.

*Occurrence.* — Lower Devonian (Emsian) from Daleszyce in the Holy Cross Mountains.

## Description

### *Fronto-ethmoidal shield*

A complete outline of the fronto-ethmoidal shield is discernible on specimens nos. 1 and 2 (pl. I A, B). It is widest on the level of preorbital corners (proc.) where it slightly (12 per cent) exceeds the length along the midline. Hence it is relatively short and broad.

The anterior margin, dorsally delimiting the mouth opening and enclosed in the subnarial corners corresponding to the posterior ends of intermaxillar elements, is sinuously curved owing to a dorsal elevation of the central portion, more conspicuously so on the sides than along the middle. This margin is thickened by a teeth-bearing lamina with the infraorbital sensory canal running along it.

The lateral margin is provided with three more conspicuous notches. The anterior one corresponds to the suture between the fronto-ethmoidal shield and the lachrymo-maxillary. The anterior, vertical margin of the lachrymo-maxillary notch is slightly damaged in all the available specimens. Probably owing thereto the writer has not been able to detect the fenestra exonarina posterior (Jarvik, 1942) although its presence is suggested by the shape of the adjacent part of the ethmosphenoid. A surface on which the lachrymal was superimposed, is situated above the posterior, horizontal part of the margin of the lachrymo-maxillary notch. The next orbital notch starts from the top of the subnarial corner, extending to the postorbital corner. There it passes into the posterior notch, narrowing the fronto-ethmoidal shield to about 56 per cent of its width on the level of the preorbital corner.

The whole surface of the imprint is closely granulated by minute pore casts indicating that the fronto-ethmoidal shield had been covered by cosmine.

Anteriorly of the lachrymo-maxillary notch is the slit-like fenestra exonarina anterior. Below it, from the subnarial corner stretches a row of pores of the infraorbital sensory canal. In its antero-medial course this canal gradually rises to the level of the anterior tip of the fenestra exonarina anterior, there passing into the supraorbital sensory canal and uniting with the rostral commissural canal. The latter descends, gently arched, in the extreme case reaching to the oral margin (spec. no 5). The course of the supraorbital sensory canal is not so readily traceable since, owing to the considerable length of the tubules and their ramification, the pores are haphazardly dispersed nearly throughout the shield surface. The position of the terminal end of the canal — before it joins the infraorbital canal — as well as that of the openings for the otical and postorbital parts of the infraorbital sensory canal (specimen no. 1), suggest that the supraorbital canal originally stretched medially from its junction with the infraorbital canal in the rostral area. Thereafter it arches laterally at some distance behind the fenestra exonarina anterior, finally to turn to the rear where it joins the postorbital and otical part of the infraorbital canal near to the posterior edge of the fronto-ethmoidal shield.

### *Sphenethmoid*

a. *Basisphenoid*. Specimen no. 6 (pl. II A) is a fragmentary basisphenoid of a large individual. The anterior part constituting the dorsum sellae, as well as a considerable upper portion, have not been preserved. The body of the basisphenoid is cylindrical, 20 mm in length and 30 mm in diameter, as measured from the caudal end which forms a concavity (cav.ch.) to fit the anterior end of the notochord. The side surface is convex anteriorly where the horizontal diameter of the basisphenoid body diminishes to 20 mm. Posteriorly it forms the basiptyergoid process (pr.bp.), 17 mm wide as measured along the vertical axis, and 10 mm long as measured along the posterior edge of the basisphenoid body. The antero-lateral edge elongates into a side lamina, afterwards arching downwards and towards the front. Thus the width of the anterior surface of the process attains 15 mm. In its latero-upper part is a coarse area for a junction with the palatoquadrate.

The antero-lower part of the process passes into the posterior part of the suborbital ledge which widens out up to 20 mm, being horizontally placed so as to support the parasphenoid. A groove occurs there between the posterior part of the supporting ledge and the body of the basisphenoid, posteriorly broad, narrowing anteriorly and medially. The groove is filled in

by a laminar tongue-like process (pr.ling.) projecting without distinct delimitation from the hind surface of the basipterygoid process. It runs along the curve of the groove towards the hypophysial opening (f.h.) on the ventral side of the basisphenoid body, at a distance of 21 mm from the posterior edge. Together with the adjacent part of the basisphenoid body it delimits the groove (sulc.aci.), which runs antero-medially. On the level of the hypophysial opening the groove is branched laterally and posteriorly (sulc.apse.) and then directed anteriorly and medially.

Above the basipterygoid process, on the lateral plane of the body, runs the broad and shallow jugular vein groove.

b. *Interorbital wall.* Both the left and the right sides of the interorbital wall are preserved on specimen no. 1 (pl. I A, II B), showing a height from 20 to 25 mm. The lower edge of the wall is slightly oblique to the ventral side of the ethmoidal region. The edge widens out laterally to form a laminar suborbital ledge, ventrally covered by the parasphenoid (pl. II B, Psph). The suborbital ledge ventrally delimits the autopalatine fossa (f.aup.) stretching over a distance of 14 mm, that is to the midlength of the interorbital wall and attaining a width (height) of 8 mm. On the level of the fossae autopalatinae the interorbital wall is extremely thin (less than 1 mm), while posteriorly it is thickened up to 4 mm on the level below the optic nerve foramen (c. II). Dorsally the fossa autopalatina is delimited by the olfactory bridge (e.olf.) and by the suspensory crest (cr. susp.). The crest is interrupted on the level opposite the optic nerve opening (o.II), where a shallow, roughly bottomed cavity (pl. II B, ar.mm.obl.) is noted. Above this area, on the interorbital wall, a small opening occurs (o.vca). On the left side of the specimen this region is somewhat damaged so that the presence of the opening could not be ascertained. The appearance of the left side, however, suggests a natural opening. Beyond the ar.mm.obl. cavity a horizontal groove extends on either side of the interorbital wall, 2 mm in diameter, running from the optic nerve opening. Beyond this the interorbital wall thickens out to 8 mm, retaining this thickness nearly to the orbital roof. There it slightly narrows owing to the presence of grooves (pl. I A, culc.o.lat.) on both sides. In the antero-upper orbital region the interorbital wall again grows thinner down to 4 mm.

Beyond the optic nerve opening, a smaller one occurs (o.III), and farther dorso-anteriorly a trace of another is detectable (o.IV?).

The above mentioned thickness of the hind-upper part of the interorbital wall depends on the presence therein of the anterior part of the cranial cavity.

c. *Orbito-nasal wall* has been preserved on specimens no. 1 (pl. II B), no. 2, partly on no. 4 (pl. IV) and, to a smaller extent, on no. 3 (pl. III).



Laterally, on the boundary of the ventral side of the ethmoidal region and the orbito-nasal wall, is a triangular area (fig. 1,2). Its sides consist of the edge of the fronto-ethmoidal shield touching the lachrymal, the postero-lateral edge of the vomeral area (*ar.Vo.*) and the lateral part of the orbito-

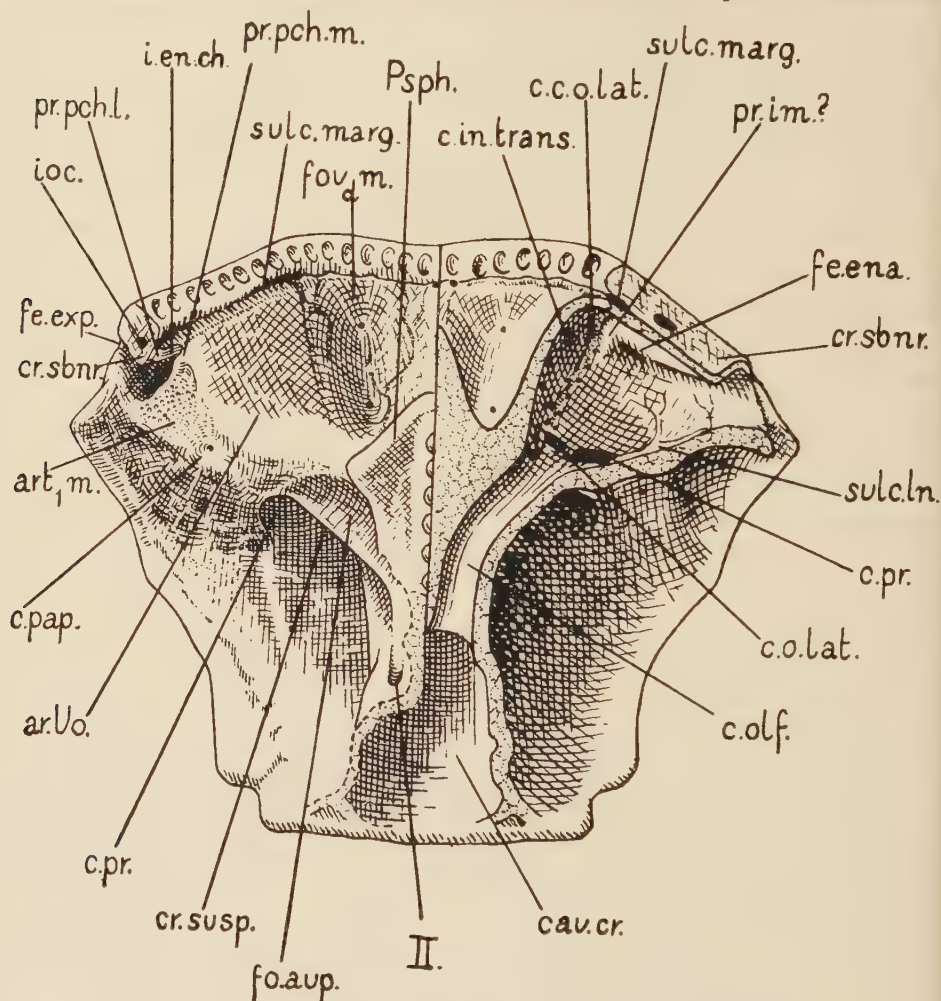


Fig. 1. — Fronto-ethmoidal shield and the ethmosphenoid, ventral view; on the left side — without basisphenoid, on the right — with removed ventral part of the ethmosphenoid

*ar. Vo.* vomeral area, *art.m* surface for processus apicalis palatoquadrati, *cav. cr.* cavum cranii, *c. in. trans.* canalis internasalis transversus, *c. o. lat.* canal for N. ophthalmicus lateralis, *cc.o.lat.* canalicules for the twigs of N. ophthalmicus lateralis, *c.olf.* canalis olfactorius, *c.pap.* canalis paraapicalis, *c.pr.* canal for N. ophthalmicus profundus, *cr. sbnr.* crista subnarina, *fe.ena.* fenestra endonarina anterior, *fe.exp.* fenestra exonarina posterior, *fo.aup.* fossa autopalatina, *fov.m.* medial depression, *inc.exch.* incisura exochoanalis, *ioc.* canalis infraorbitalis, *pr.im.* processus intermedius? *pr.pch.l.* processus parachoanalis lateralis, *pr.pch.m.* processus parachoanalis medialis, *Psph.* parasphenoidium, *sulc.ln.* sulcus lateralis narium, *sulc.marg.* sulcus marginalis, *II* outlet of N. opticus.

-nasal wall. The lateral part of this area contains the great fenestra nasalis posterior communis (fig. 1,2; pl. II B; *fe.npc.*). This is slightly elliptic, with two ventro-lateral notches, giving a subcordate outline to the whole opening. The transverse diameter of the opening in specimen no. 1 is 3 mm. Laterally it is delimited by the outer enchondral wall of the nasal cavity and the adjacent part of the fronto-ethmoidal shield. On the level just above the palatal lamina of the fronto-ethmoidal shield (*la.pal.*), the enchondral wall grows thinner owing to stronger penetration of the recess (*rec.tnp.*), whose distal end approaches to the edge of the fronto-ethmoidal shield. Ventrally the recess — *rec. tnp.* — and the notch — *i.enp.* — are delimited by the palatal list of the fronto-ethmoidal shield (*la.pal.*) and by the enchondral wall of the nasal cavity enveloping it dorsally. The medial edge of the above mentioned palatal list, together with adjacent part of the enchondral nasal cavity wall, laterally delimit another notch — *i.ench.* — of fenestra nasalis posterior communis, situated directly above the notch — *i.exch.* — within the postero-lateral margin of the vomeral area. Medially the endochoanal notch (*i.ench.*) is delimited by the small

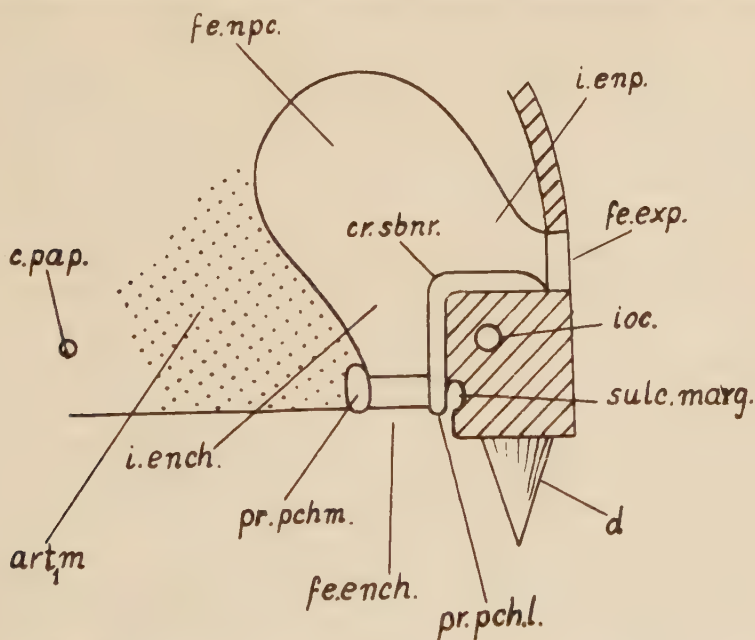


Fig. 2. — Diagrammatical drawing of the region of fenestra nasalis posterior communis

*art1m* surface for the processus apicalis palatoquadrati, *c.pap.* canalis paraapicalis, *cr.sbnr.* crista subnarina, *d* grasping tooth, *fe.ench.* fenestra endochoanal, *fe.enp.* fenestra exonarina posterior, *fe.npc.* fenestra nasalis posterior communis, *i.ench.* incisura endochoanal, *i.enp.* incisura endonarina posterior, *ioc.* canalis infraorbitalis, *pr.pch.l.* processus parachoanal lateralis, *pr.pch.m.* processus parachoanal medialis, *sulc. marg.* sulcus marginalis, dermal bones (fronto-ethmoidal shield) — stippled.

medial parachoanal process (pr.pch.m.), while the fenestra nasalis posterior communis is delimited by the edge of the coarse area for the processus apicalis palatoquadrati (art<sub>1</sub>m). This area is in the shape of a trapezoid, with the longer base facing the fenestra nasalis posterior communis. In specimen no. 1 the base is 4 mm long. Farther medially from the surface for the processus apicalis, in the median angle of the triangle constituting the here described area, is a fair-sized opening of the canal entering into the nasal cavity (c.pap.). This canal runs from the rear and laterally towards the front and medially, as is readily seen in specimens nos. 1 and 3 (pl. III A). Two smaller openings are seen in the outer-upper corner of the here mentioned area in a process by Jarvik (1942), referred to as the "ventro-lateral process of the postnasal wall" (pr.vl.).

Medially of the above described triangular area, the lower part of the orbito-nasal wall forms a cavity (fig. 1; pl. II B; fo.aup.), delimited dorsally by the crista suspendens. They are arched, posteriorly passing into the interorbital wall. Above the olfactory ridge there is a depression containing a large opening at the bottom (c.pr.). A groove (sulc.o.lat.) running on the boundary line between the interorbital wall and the orbital roof is directed towards this opening, as is seen in specimens nos. 1 and 2 (pl. I). On the left side of specimen no. 1 the groove may have stretched to another somewhat smaller opening (c.o.lat.), situated more dorso-medially, similarly as on specimen no. 4 (pl. IV). No other, fairly large openings have been ascertained on the orbito-nasal wall. Only on specimen no. 4 the openings of the very minute canaliculi are detectable in the upper-lateral part of the orbito-nasal wall. Since these canalicules do not penetrate into the nasal cavity, they are to be regarded merely as foramina nutritii.

d. *Ventral side of the ethmoidal region* (fig. 1; pl. II B; pl. III C) is trapezoidal, 14 mm high on specimen no. 1. In the same specimen the longer base, corresponding to the postero-ventral edge of the ethmoidal region, has a length of 42 mm. The opposite flank, together with the lateral sides forming the dorsal boundary of the mouth opening, is 20 mm long. This surface is delimited on the outside by the protruding, step-like, tooth-bearing edge of the fronto-ethmoidal shield (la.pal.).

In the medial part, a pair of symmetric, elliptical medial depressions (fov<sub>d</sub>m. = "cavum internasale" of Jarvik, 1942) occurs on the ventral side of the nasal region. They are separated by a crest (cr.m. — crista mediana = "internasal ridge" of Jarvik, 1942) running in the midline. While in specimen no. 1 these depressions are nearly perfectly elliptic (with length 10 mm, width 5 mm, depth 4 mm), similarly as in *Porolepis "spitsbergensis"*, in specimens nos. 3 and 4 anteriorly they expand much farther, rather approaching *P. "brevis"* and *P. "elongata"*. In specimen no. 3 their length



is from 8 to 9 mm, while the average width is 6 mm and a depth of about 4 mm. In the distinctly larger specimen no. 4 the width is 18 mm, with depth at least 7 mm, while the moderate-sized specimen no. 5 shows a width of 7 mm. Laterally of the medial depressions (fov<sub>d</sub>m.) occur the four-sided areas occupied by vomers (ar.Vo.). These are slightly roof-domed, with one plane descending to the front towards the above mentioned depressions, while the other plane is gently convex, posteriorly inclined. The vomeral areas correspond simultaneously to the bottom of nasal cavities (solum nasi). The postero-medial margin is indicated as an edge passing into a crest, arcuately directed towards the ventral margin of the interorbital wall and passes into the "suborbital ledge". In the medial part the postero-lateral edge of the vomeral area ventrally delimits the above described coarse surface of the processus apicalis palatoquadrati (art<sub>1</sub>m). Farther laterally it forms a rather small semielliptic notch (i.exch.), bilaterally rimmed by the parachoanal processes (pr.pch.l. and pr.pch.m.). A somewhat larger lateral parachoanal process (pr.pch.l.) passes throughout its dorsal length into a horizontal enchondral lamina. This constitutes that part of the nasal cavity wall which rests on the dorsal side of the palatal ledge of the fronto-ethmoidal shield (la.pal.).

A marginal groove most readily discernible on specimen no. 3 (pl. III C), runs along the inner protruding, step-like margin of the fronto-ethmoidal shield on the ventral side of the nasal region. Some parts of this groove are closed up into a canal by the palatal lamina of the fronto-ethmoidal shield and the anterior part of the ethmosphenoid. Near the antero-lateral corner of the vomeral area (ar.Vo.) this groove gives a branch leading into a slightly smaller opening. Being now notably narrower, the groove — sulc. marg. — continues along the margin of the fronto-ethmoidal shield, anastomosing with a similar opposite groove. Along the course of the anastomosis small openings are discernible leading into the interior between the fronto-ethmoidal shield and the adjacent enchondral part. After branching off the anastomosis the groove becomes all the more shallow. It stretches along the edge of the median crest (cr.m.) forming minute ramifications directed to the bottom of the medial depression and there producing a network. The other groove ramification, branching off at the antero-lateral corner of the vomeral area (ar.Vo.), extends directly towards the medial depression. At the bottom of the depression small openings are discernible on specimen no. 3 (pl. III C), one of them at the anterior, the other on the posterior end of the depression (c<sub>v</sub>n-b?).

e. *Cranial cavity.* Casts of the anterior part of the cranial cavity are preserved on specimens nos. 1 and 2 (pl. I, II), where we can discern the lower part and the antero-upper recess. The latter is in the shape of a sac-

like chamber, with more or less uniform width. In specimen no. 1 the average width is 7 mm, with length of 20 mm. The fronto-upper recess expands somewhat more in the posterior part only, forming secondary diverticles. The anterior end is dorsally somewhat differentiated and its surface displays traces of bipartition and corrugation. In specimen no. 1 it protrudes anteriorly approx. 5 mm beyond the level of the outer optic nerve foramen, hence it does not attain to the level of the orbito-nasal wall. In specimen no. 2 it is damaged. The lower part of the cranial cavity terminated at a distance of approx. 5 mm behind the level of the external optic nerve openings, passing into two canals (c.olf.), each 3 mm in diameter. These at first run parallel to each other beneath the anterior part of the anterior-upper recess, and then diverge laterally inside the already described olfactory ridges (e.olf.), to open finally into the medio-posterior ends of the nasal cavities beneath the o.pr.foramen.

A shapeless imprint (pl. I, B, x), extending to the level of the orbito-nasal cavity (seemingly a prolongation of the cranial cavity), occurs in specimen no. 2 between the casts of olfactory canals. The ventral face of the ethmosphenoid in this specimen, however, was broken off before being covered up by sediment. Hence, the just mentioned imprint is nothing more but a trace of the damage. This is likewise suggested by its irregular surface and fusion with the olfactory canals which are distinctly bounded in specimen no. 1.

f. *Nasal cavity.* The nasal cavities, situated in the lower part of the nasal region, beneath the vomeral area (fig. 1; pl. II B; pl. III C; ar.Vo.), are onion-shaped or conical, with the apex facing postero-medially, while the base is turned antero-laterally and somewhat dorsally. The postero-lateral part of the nasal cavity elongates into a large canalis nasalis posterior communis (fig. 3, c.npc.), running postero-laterally and ventrally. It opens up as the above described fenestra nasalis posterior communis (fig. 3; pl. II B, fe.npc.). A slit-like fenestra endonarina anterior (fig. 1, 3; pl. II B, fe.ena.), leading into the anterior nasal canal, occurs in the middle of the antero-lateral nasal cavity wall. Anteriorly this fenestra is delimited by a small ridge (pr.inf.?) widening out towards the bottom. Ventrally it rims the fenestra endonarina anterior and is directed backwards, passing without distinct boundaries into a crest (cr.sbnr. — crista subnarina = "crista rostro-caudalis" of Jarvik, 1942).

This crest consists of the palatal lamina of the fronto-ethmoidal shield lined by a thin enchondral wall. It causes the differentiation of two recesses in the canalis nasalis posterior communis. The upper side recess corresponds to the i.enp.notch and may be called the recess for the posterior nasal tube. The lower medial recess leads to the endochoanal notch (i.ench.)

and represents the choanal recess. A much narrower and less conspicuous crest (*cr.or.*) stretches along the border between the antero-lateral and the ventral walls of the nasal cavity. It starts laterally to the summit of the endochoanal notch and terminates slightly below and a little to the front of the fenestra endonarina anterior.

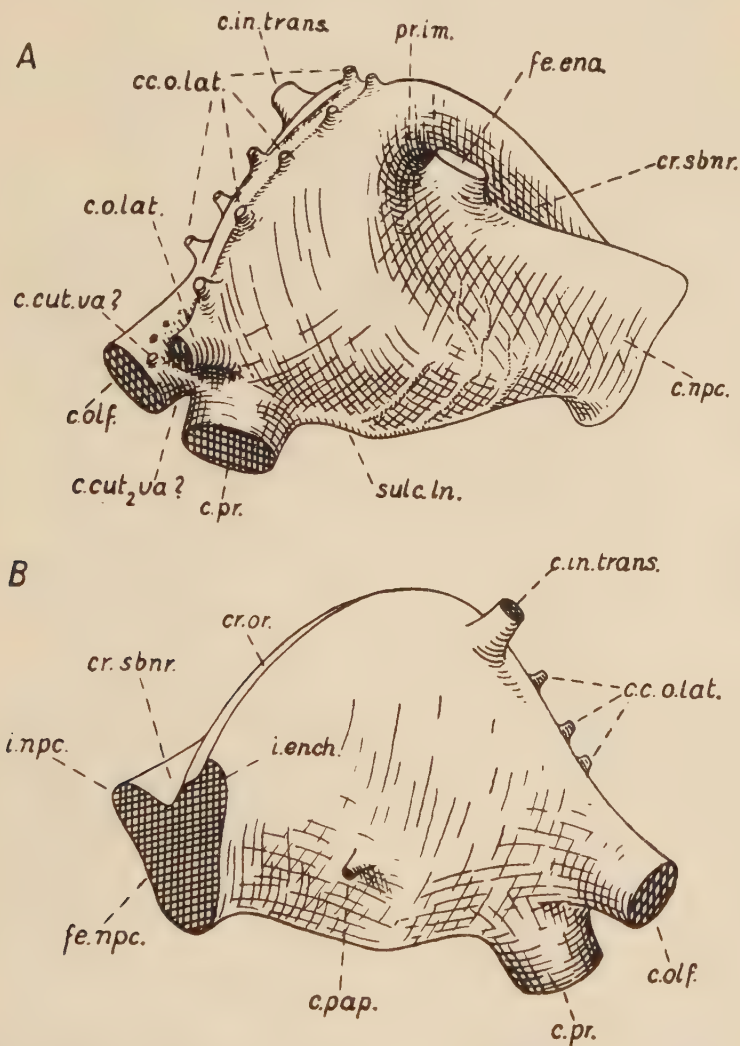


Fig. 3. — The cast of the right nasal cavity: A dorsal view, B ventral view

*c.in.trans.* canalis internasalis transversus, *c.npc.* canalis nasalis posterior communis, *cc.o.lat.* canalicules for the twigs of N. ophthalmicus lateralis, *c.cut.va?* canal for the presumed cutaneous vein, *c.cut<sub>2</sub>va?* groove connecting the profundus canal with the *c.cut.va?* opening, *c.o.lat.* canalicules for N. ophthalmicus lateralis, *c.olf.* olfactory canal, *c.pap.* canalis paraapicalis, *c.pr.* canal for N. ophthalmicus profundus, *fe.ena.* fenestra endonarina anterior, *i.ench.* incisura endochoanal, *i.npc.* incisura endonarina posterior, *i.oc.* canalis infraorbitalis, *prim.* processus intermedius?, *sulc.ln.* groove for ramus lateralis narium, *cr.or.* crista orbitorostralis.



In the medio-posterior extremity of the nasal cavity occurs a fair-sized olfactory nerve foramen (I), in specimen no. 1, with a diameter of 3 mm. Above it, somewhat to the side, is another opening with similar diameter (c.pr.), connecting the nasal cavity with the orbital. In specimens nos. 1 and 2 a groove (sulc.o.lat.) leads into that foramen, running on the boundary between the interorbital wall and the orbital roof (pl. I A). In specimen no. 4 (pl. IV) this groove penetrates by a separate opening (c.o.lat.) into the nasal cavity, medially and slightly dorsally of the o.pr. opening. From the latter opening a groove (sulc.ln.) runs laterally on the posterior nasal cavity wall; along its course it gives off numerous minute branches which in their turn ramify on the adjacent walls of the nasal cavity. The other groove (c.cut.<sub>2</sub>va?) is directed medially above the olfactory nerve foramen, close to which one of the main groove ramifications penetrates into the nasal cavity wall through the c.cut.va? opening. Another ramification of the main groove (sulc.mn.) continues its course along the boundary between the medial and dorsal walls of the nasal cavity. Several small openings, piercing the roof of the nasal cavity, occur along that groove. They start from the c.o.lat. opening (if this is present as in specimen no. 4), or from the o.pr. opening (as in specimens 1 and 3). One of these foramens, slightly larger, occurs beneath the groove (sulc.mn.) and leads to the transverse canal connecting the two nasal cavities, as is shown in specimen no. 4 (pl. IV). In specimen no. 3 this canal apparently communicates with the c<sub>v</sub>n-b? opening in the domed bottom of the medial depressions (fov<sub>d</sub>m., pl. III A).

### *Parasphenoid*

The only preserved fragment of the parasphenoid is the anterior part resting on the suborbital ledge (specimen no. 1). As is common in *Porolepis* it is slender and narrow, the width in this case being slightly below 10 mm. The anterior end forms an angle with the anteriorly facing apex and slightly encroaches the posterior part of the ventral face of the ethmoidal region, just behind the medial depressions (fov<sub>d</sub>m). A crest, bearing a longitudinal row of denticles, extends along the central line on the ventral face of the anterior part of the parasphenoid.

### *Lower jaw*

Specimen no. 7 (fig. 4; pl. V A) represents a large fragment of the left lower jaw of a giant individual. On the level of the anterior end of the prear-

Fig. 4. — Latex cast of lower jaw (specimen no. 7); nat. size

Co<sub>1</sub>, Co<sub>2</sub> coronoids, d grasping teeth, De dentale, fov<sub>r</sub>. depressions remaining after resorption of the grasping teeth, fo.add. adductor fossa, for.Meck. foramen Meckeli (s. meckelianum), fov<sub>d</sub>1, fov<sub>d</sub>2 pits of the upper grasping teeth, Id<sub>1</sub>, Id<sub>2</sub> infradentals, o. opening for a vein, pl.mntm. concave surface of the mentomandibular, sulc.v. groove for a vein, Prart. prearticular

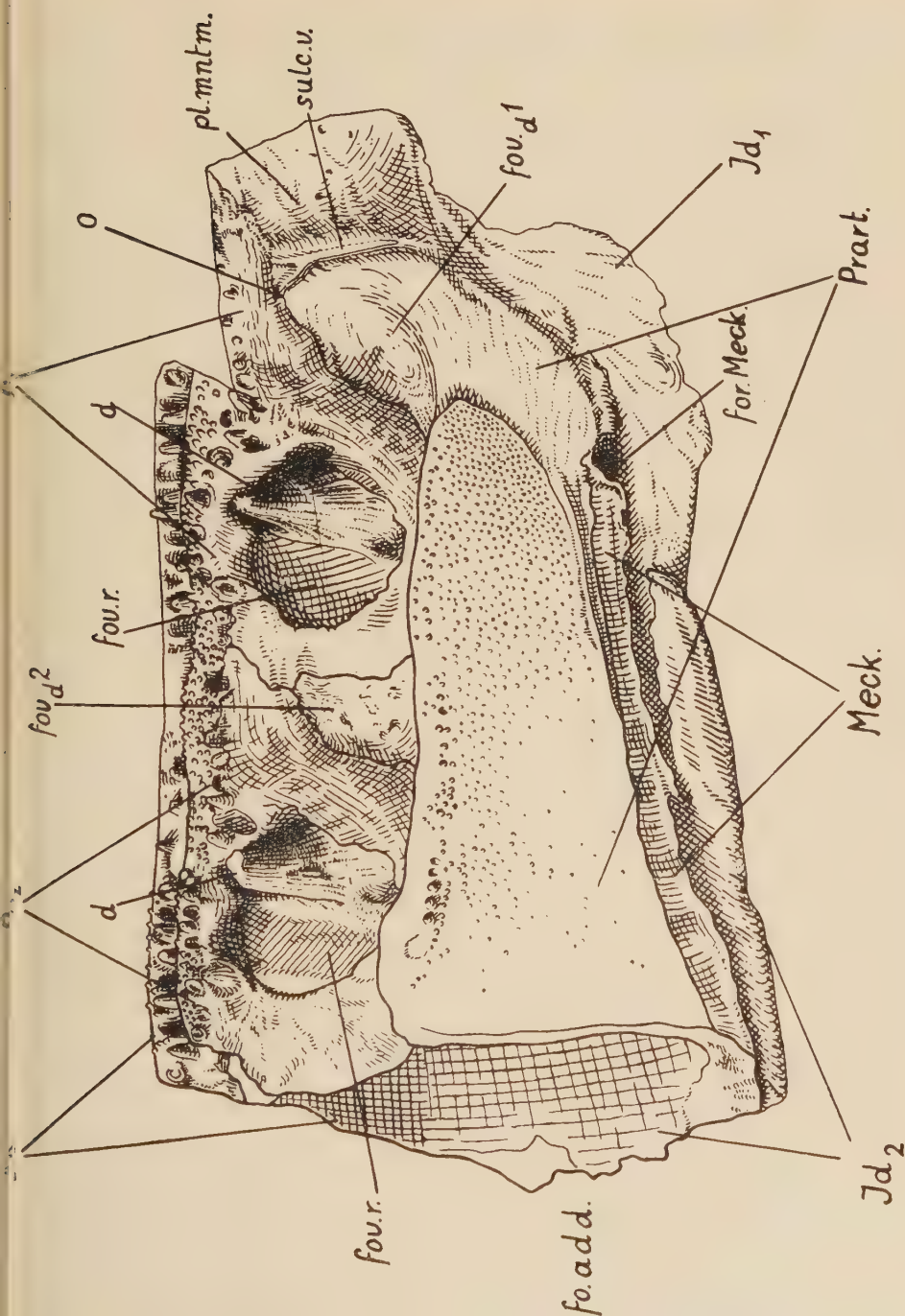


Fig. 4. — Explanation on the opposite page (bottom).

ticular its width is 73 mm, stretching 88 mm beyond the posterior margin of the intercoronoid. The whole fragment is 155 mm long. It shows the inner surface of the jaw. The lower-medial margin is formed by infradentals 1 and 2 (splenialia), whose boundaries are not visible. A more complete infradental on the smaller specimen no. 8 (pl. V B), (length 52 mm, 15 mm anterior width, 22 mm posterior width), indicates that this element stretched to the symphysis. A moderately high wall (7 mm in specimen no. 7), formed by the here uncovered lamina of the Meckelian bone (Meck.), rises steeply above the level of the infradentals. On a level just beyond the anterior end of the tooth-bearing prearticular face a large opening occurs in the Meckelian bone (with a 7 mm diameter in specimen no. 7), leading into the adductor fossa (for. Meck.). Further to the front the Meckelian bone is compressed and forms the symphyseal part, i.e. the mentomandibular. In this region it is hardly possible to distinguish the Meckelian bone from the prearticular. It seems, however, that the prearticular did not reach to the symphysis, leaving uncovered a fair sized concave surface, formed by the mentomandibular. Numerous traces of vascular branches, running to the afore mentioned groove, occur on this surface which is posteriorly bounded by a transverse groove (sulc.v.), forking laterally and penetrating by openings (o.) below the anterior procoronoid process. The free part of the mentomandibular, incomplete in specimen no. 7, is wholly visible in specimen no. 8. Here, on the anterior, bluntly truncated end, we can see the symphyseal face, suboval in outline.

The prearticular is posteriorly raised rather high (19 mm in specimen no. 7) above the medial surface of the outer maxillary wall. Anteriorly it descends gently tapering to form a tongue-like area, with minute shagreen denticles disseminated on it. A row of larger denticles stretches along its outer lateral margin. In specimen no. 7 the last denticle is over 5 mm high, with a basal diameter of 2.5 mm. Anteriorly the prearticular forms an unornamented area, gently inclined medially and steeply descending to the sides. Together with the adjacent procoronoid it forms here a depression to house the upper grasping teeth (fov<sub>d1</sub>). The bottom of this cavity, anteriorly bounded by the afore described groove (sulc.v.), seemingly represents the uncovered Meckelian bone area.

All the coronoids are ring-shaped, with the anterior process running parallel to the outer margin of the jaw. Hence the coronoids constitute an unbroken lateral boundary, along which there are rows of larger and smaller marginal denticles. In specimen no. 7 the larger ones attain a height of 5 mm, with basal diameter of 3.5 mm. Their walls display fine striation. The procoronoid meets the antero-lateral face of the mentomandibular by its anterior process, while every other process meets an anterior element.



In the remaining area the coronoids are mutually separated, bounding cavities for reception of the grasping teeth. The centres of the coronoids are occupied by pits receiving the larger grasping teeth. In specimen no. 7 they display an average height of 22 mm, and a basal width of 10 mm. They are slightly incurved. This surface is delicately striated suggesting a corrugated wall. Small circular pits (with a diameter of 7 mm in specimen no. 7) are seen on the medial side of the preserved coronoid bases. The distal ends of the dental cavities in coronoids are empty places after the lost grasping teeth. They were coated by a fine osseous layer, or even revealed the uncovered Meckelian cartilage. Specimens nos. 7 and 8 contain casts of the adductor fossa which resembles that described by Gross (1941). It differs, however, in the forward elongation stretching farther below the prearticular. Narrowing more strongly and curving medially, this fossa opens outside by the afore described aperture in the medial wall of the Meckelian bone. The width of the adductor fossa behind the intercoronoids is here 73 mm. After 90 mm of a forward course it narrows to 17 mm, whereafter it bends medially in a funnel-like terminal part. Specimens nos. 9 and 10 (pl. V C, D) do not add any new details besides those provided by specimens nos. 7 and 8. Fragments nos. 11 and 12 only show imprints of the outer surface, coated by a typical cosmine sheath.

### Dentition

The described material comprises a number of detached teeth of various size (pl. VI). The grasping teeth are conical, slightly sigmoidal, with medially directed tips. The medial face of each grasping tooth, if complete, is provided with a saucer-shaped cavity, which probably represents a pressure mark, made by a tooth of the following generation. One of the grasping teeth (pl. VI, 21) attains a length of 37 mm, with a basal width (sagittally) of 23 mm. Tooth no. 14 (pl. VI, 23), with medial length of 20 mm, is equally stumpy; its outer labial length is smaller, the basal width being 22 mm. In both these teeth the dumpiness is due to the wearing off or damage of the dental tips. Tooth no. 15 (pl. VI, 22), nearly complete, is 25 mm high, with a basal width (sagittally) of 13 mm, that vertical to the sagittal being 7 mm. Since dental section in the genus *Porolepis* is usually subcircular, the difference of diameters here is probably due to compression. The true diameter is somewhere between the two figures. Other teeth, more complete and not disfigured, are rather slender though strongly expanded at the base. The outer surface of teeth is covered by flat broad ribs, separated by fine grooves, which give an appearance of longitudinal bands. In the lower portions the ribs are frequently subdivided by secondary minute grooves. The size ratio of the various tooth categories in one indi-

vidual is shown in specimen no. 7, which represents a fragmentary lower jaw. The grasping teeth here are 30 mm long medially, 16 mm labially, with a maximum sagittal diameter of 10 mm. The marginal teeth on the coronoids and on the dental attain a length of 7 mm, with a width (section diameter) of 3 mm. Similar dimensions are attained by teeth of the marginal row of the prearticular.

### *Scales (pl. VI)*

Scales vary strongly in shape and size. All possible transition forms are encountered, from those symmetrically rhomboid to asymmetric and rounded ones. An elongated cavity may sporadically occur in the basal area, which is as a rule smooth, but an elevation or a rib may occur too. On the outer surface the free part is frequently separated from the overlapped portion by a distinct groove. The free portion of the scale is evenly coated by dentine, pierced by minute pores. At the anterior border the coating of dentine and enamel is marked all over by ribs, separated by grooves with pores. These ribs have usually a parallel arrangement, sometimes however they converge towards the centre of the proximal free surface border. Others are forked or taper forwards. The length of ribs varies too. In one specimen they occupy  $1/3$  of the total uncovered area, in another they are nearly altogether absent, as is commonly seen in one of the margins of asymmetric scales. The ribbing also displays a wide scale of passages, from extremely fine striation to thick, sharp and distinctly marked ribs. This is not, however, in any way correlated with the size of scales. On a large scale (pl. VI, fig. 10) the ribs may be very faint, or be strongly developed on a distinctly smaller scale (pl. VI, fig. 4). On some specimens (pl. VI, fig. 1, 12) the anterior ends of ribs are underdeveloped and replaced by tubercles resembling those in *Glyptolepis*. The behaviour of the overlapped scale area varies too. In symmetric rhomboid scales it is symmetric too, mostly broad (up to  $1/3$  of the overall length of scale); in asymmetric scales one area is broader and usually more strongly curved. On one specimen the overlapped area is very narrow, hardly  $1/9$  of the scale length. On another specimen (pl. VI, fig. 2) an embayed notch is visible on the anterior border of the free area, due to an extremely shallow course of the sensory canal. Scale dimensions in the described material range from 6 to 35 mm.

### *Closely indeterminate elements*

Specimen in pl. VI, fig. 16, probably represents a fragmentary shoulder girdle (clavicle?). Roundish and longitudinal pits are visible on it. As compared with specimens from the Rhine province, a notably larger surface is here coated by a sheath of dentine and enamel. A similar net-work of

ribs is discernible on specimen no. 22 (pl. VI, fig. 17), whose identification is doubtful. It may represent a fragmentary gular bone. Here the dentine sheath coats a narrow marginal strip only.

## DISCUSSION

### aa. *Ethmosphenoid*

This element is apparently short in *Porolepis* as compared with the ethmosphenoid of *Eusthenopteron*. While in the latter genus the height/length ratio is 1 : 3, that in *Porolepis* was approx. 1 : 2.

The ethmoidal area is broad, short and bluntly terminated. The ventral face of the ethmoidal region is somewhat oblique to the ventral face of the interorbital wall.

The basisphenoid (pl. II A) is short too, the processus connectens poorly developed, resembling that in *Eusthenopteron*. Large processes of processus basiptyergoideus (pr.bp.) with an ear-like area for connection with the palatoquadrate occur on the lateral surface of the body. The latter is posteriorly provided with a characteristic concavity to receive the end of the dorsal chord. The lower parts of the processes elongate downwards and forward to form the posterior portion of the suborbital ledge. In opposition to *Eusthenopteron* where the ledge narrows gradually to the front, in *Porolepis* it retains a uniform width as far as the level of the hypophysial opening (f.h.), thus forming a support for the broad posterior part of the parasphenoid. Between this support and the core of the basisphenoid occurs the process (pr.ling.), projecting from the basiptyergoid process. It bounds a groove, locally closed up into a canal (sulc.aci.) which, at the level of the hypophysial opening, gives off branches directed laterally and backward (sulc.apse.). As is suggested by the description and figure of the parasphenoid and the adjacent portion of the basisphenoid in the genus *Glyptolepis* (Gross, 1936, p. 148-151, fig. 10 A-C), the grooves (sulc.aci.) gave off a secondary branch, directed laterally to the front (sul.pal.). The two branches then united and entered the interior of the skull by openings in front of the hypophysial opening. The ventral side of the sphenoidal region of the genus *Porolepis* differs from the corresponding region in *Eusthenopteron* in that the canals, here transmitting vessels, are closed up by the parasphenoid and the adjoining part of the basisphenoid, not to speak of the presence of the broad ledge supporting the parasphenoid.

The interorbital wall is widest in the upper-hindmost quarter of the orbit, in agreement with the shape of the enclosed cavities and canals which will be discussed here below. It is just as broad on the boundary between the front-upper and the front-lower quarters, owing to the ridge-like eminences (e.olf.), which stretch here, horizontally arched, indicating



the course of the olfactory canals. The crest (crista suspendens), occurring on these eminences, is broken up in its distal end by a gently concave, bipartite, coarse area, doubtlessly corresponding to the attachment place of the oblique eyeball muscles (ar.mm.obl.). Somewhat higher up and farther backwards, on the level of the posterior end of fossa autopalatina (f.aup.) occurs the optic nerve opening (o.II). As compared with other crossopterygian fishes, among the Holoptychiidae and the Rhizodontidae as well as Actinistia, this opening is relatively small in *Porolepis*. From it a groove is directed anteriorly, with the same diameter, corresponding to the optic nerve running here immediately after being emitted from the skull and before taking a lateral course towards the eyeball. A smaller opening, most likely corresponding to the outlet of the oculomotor nerve (o.III), occurs behind the optic nerve opening and somewhat dorsally.

A minute aperture, not observable in the majority of Rhipidistia, is present a little more to the front on the olfactory eminence (e.olif.), above the oblique eyeball muscles area. It is certainly a natural opening; since it leads into the olfactory canal, its presumable function was to transmit the vein — vena cerebialis anterior (o.vca.). This vein has likewise persisted in *Rhizodopsis* (Säve-Söderbergh, 1930) among the Rhipidistia, also in *Latimeria* (Millot & Anthony, 1958) among the Actinistia.

The doubtful opening (o.IV?) in front of the oculomotor nerve outlet may have transmitted the nerve N. trochlearis.

In *Porolepis*, similarly as in *Latimeria* (Millot & Anthony, 1958), it has not been possible to ascertain a separate opening for the a. ophthalmica magna.

The pituitary vein opening (v.pit.) occurs quite close to the anterior border of the basisphenoid.

A large opening for the N. ophthalmicus profundus (c.pr.) occurs on the orbito-ethmoidal wall, above the olfactory eminence. The groove transmitting the N. ophthalmicus lateralis (sulc.o.lat.) is occasionally likewise directed into this opening. Elsewhere the latter nerve enters into the nasal cavity by its own opening (c.o.lat.), situated dorsally and medially in relation to the N. ophthalmicus profundus. In the ventro-lateral side of the just mentioned wall there is a small opening (c.pap.) of indeterminate function, and laterally of it, is an area (art.im) for junction with the processus apicalis, which belongs to that part of the palatoquadrate referred to as pars autopalatina. The character of this area suggests a synchondrotic junction with the palatoquadrate, similarly as in *Eusthenopteron*. The small openings pitting this area are most likely nothing more but the foramina nutricia, since it is impossible that any important nerves or vessels were transmitted through the joining surface. The fenestra nasalis posterior communis (fe.npc.) is placed outside the area for the processus apicalis. Two notches occur in the ven-

tral side of this opening. The medial one (incisura endochoanalis, i.ench.) extends ventro-medially to the palatal lamina of the ventral margin of the fronto-ethmoidal shield, and above the groove leading to the notch (i.exch.) on the postero-ventral margin of the orbito-nasal wall. This groove is rimmed by the medial and lateral parachoanal processes (pr.pch.m., pr.pch.l.). As is suggested by the position of the area for the processus apicalis, the whole fenestra nasalis posterior communis, or its greater part beyond the choanal notch, occurred above the dorsal surface of the palatoquadrate. Communication with the oral cavity was possible for the choanal notch only, by means of the just mentioned groove. Thus the internal nostrils occupied about a minor part of the fenestra nasalis posterior communis. Its lateral notch (incisura endonarina posterior, i.enp.) occurs above the palatal lamina of the fronto-ethmoidal shield, and is directed outside towards the place, where Jarvik (1942) puts the incisura exonarina posterior (i.exp.) of the fronto-ethmoidal shield.

The posterior nasal tube and the choanal duct did not completely fill up the fenestra nasalis posterior communis. Hence arises the question as to the function of the remaining considerable portion of that opening. As compared with the corresponding cranial region of other Rhipidistia crossopterygians, it may be ascertained that the here considered portion of the fenestra nasalis posterior communis, owing to its position above the level of the dorsal face of the palatoquadrate, corresponded to the independent opening in the orbito-nasal wall of *Eusthenopteron*. According to Jarvik (1942), this opening corresponded to the naso-lachrymal duct and the trigeminal nerve, i.e. the ramus infraorbitalis. Apparently there is no sound reason to prevent the assignment to the same function to the major dorsal portion of the fenestra nasalis posterior communis in *Porolepis*. This differs from the corresponding opening in *Eusthenopteron* only in that it is not delimited by the skeletal bridge from the area, corresponding to the choanals and leading to the posterior external nostrils. In consequence of such an interpretation of the dorsal side of the fenestra nasalis posterior communis in *Porolepis* we must accept that the considered opening in *Eusthenopteron* cannot correspond to the posterior nostrils. It still remains to be determined, whether it actually pertained to the naso-lachrymal duct. And here again the question arises as to the position in *Eusthenopteron* of the element truly equivalent to the posterior external nostrils. This seems most likely to be the small opening in the orbito-nasal wall, by Jarvik (1942) referred to as the „opening for r. buccalis lateralis” (f.buc.). Similarly as the fenestra endonarina posterior in *Porolepis*, this opening is dorso-laterally situated in relation to the choana, above the palatal lamina of the fronto-ethmoidal shield and the palatoquadrate, and at the same time in the proximity of the lacrimale.

The central portion of the ventral face of the ethmoidal region in *Porolepis* is taken up, throughout its length, by oval medial depressions (fov<sub>dm</sub>), separated by a crest — crista mediana (cr.m. = „internasal ridge” of Jarvik, 1942). These cavities were originally regarded (Stensio, 1932; Holmgren & Stensiö, 1936) as dental pits to lodge the grasping teeth of the posterior coronoids. After it had been proved that teeth lying on coronoids could not reach to the just mentioned depressions, Jarvik (1942) postulated that they housed an intermaxillary gland. In *Porolepis*, similarly as in *Urodela*, this gland was supposed to be paired and to open up by numerous ducts, in opposition to that same gland in *Eusthenopteron* which was supposed to be unpaired, with one duct only, as in *Anura*.

According to Schmalhausen (1958), the unpaired intermaxillary gland is encountered in *Urodela* as well as in *Anura*. In *Anura* it occurs among the upper processes of the premaxillary bones and opens up either by numerous independent ducts (in primitive forms), or by ducts entering the transverse groove or paired pit (in more advanced forms). In *Urodela* this gland penetrates between the nasal sacs, sometimes reaching the dorsal side of the head. Numerous ducts open up on the palate within a small depression. In more advanced forms this depression is stretched into an elongated canal. In *Apoda* the intermaxillary gland consists of the glandular area in the posterior part of the palate.

In the lack of fundamental structural differences of the intermaxillary gland and in view of its complete homology, as ascertained by Schmalhausen in *Anura* and *Urodela*, this element loses its significance for the problem regarding the independent origin of stocks, to which *Porolepis* and *Eusthenopteron* are referable and, furthermore, as regards the polyphyletic or monophyletic origin of amphibians.

The dispersed type of the intermaxillary glands is doubtlessly the most primitive one and was certainly common in primitive amphibians. It is this type of glandular structure that may be expected in crossopterygians, from whom the amphibians have descended — if this gland existed there at all. It is hardly probable that cavities of such considerable size, as those encountered in the centre of the ventral side of the ethmoidal region in *Porolepis*, could have been formed for the area of dispersed glands. Even if, in *Porolepis*<sup>1</sup> as in *Eusthenopteron*, the medial part of the dentale did not bear teeth, surely the ancestors of these forms did possess them, since grasping teeth are encountered on the anterior end of the dentale in other representatives of the crossopterygians, e.g. in *Panderichthys*. It is not, therefore, out of the question that the cavities on the ventral face of the ethmoidal re-

<sup>1</sup> According to Prof. E. Jarvik's kind communication, some dental structures have been detected by him in the symphysial part of a lower jaw in a relatively closely allied form; they will be described in one of that author's next papers.



gion — independently of their shape — may represent remnants of the original conditions. If so, Stensiö's interpretation (1932) would seem the more probable one, except that the medial depressions would then correspond not to the grasping teeth of the procoronoids, but to those in the symphyseal part of the lower jaw. The poor development of the „prenasal pits” (Jarvik, 1942) in *Eusthenopteron* would suggest their vestigial condition owing to the loss of the symphyseal teeth on the dentale. The homology of the „prenasal pits” in *Eusthenopteron* with the „internasal pits” in *Porolepis* is moreover suggested by the presence in both forms of openings, probably transmitting the same twigs of vessels and nerves (terminal twigs of r. medialis narium?).

Areas, on which the vomers are resting (ar.Vo.), occur laterally of the here discussed medial cavities. In *Porolepis* these areas are rather distant from each other, owing to the poor development of the nasal cavities, and the strong development of the medial depressions. It should be here noted that, both in *Eusthenopteron* and in *Porolepis*, the vomeral area at the same time constitutes the bottom (solum nasi) of the nasal cavities. The greater proximity of the nasal cavities in *Eusthenopteron* is correlated with the arrangement of the vomers, which meet here in the central line over a considerable length. In *Porolepis*, the distance between the vomers, as well as between the nasal cavities, is considerable. The smaller length of the vomers, as well as of the N. palatinus VII canals in *Porolepis*, is surely referable to these differences in the development and arrangement of the nasal cavities and vomers, and to the general proportions of the anterior end of the snout.

A groove, partly closed up into a canal (sulc. marg.), occurs along the lateral and anterior borders of the here adjoining fronto-ethmoidal shield. This groove merges with a similar groove of the opposite side and gives off branches, leading into the openings between the fronto-ethmoidal shield and the adjacent part of the ethmosphenoid. Several ramifications of the just described groove descend into the interior of the medial cavity, merging with the net-work of grooves at its bottom and with the opening discernible there. The marginal groove (sulc. marg.) must have transmitted the nerve twig arising at the N. maxillaris, together with the accompanying vessels.

## b. Cranial cavity

The part of the cranial cavity, occupying the interior of the interorbital wall, was divided into two portions: the ventral stretching to the olfactory canals, and the antero-dorsal recess. The here studied specimens do not provide reliable suggestions as to the boundary lines of these two divisions. The delimitation of the anterior quarter of the antero-dorsal recess (rec.pin.), however, is beyond doubt. It certainly corresponded to the pineal recess, likewise encountered in *Eusthenopteron* (Jarvik, 1942, fig. 57, c.pin.). Such

an interpretation is suggested by the fact that the cast of the recess terminates in a place exactly corresponding to that of the pineal depression on the ventral face of the fronto-ethmoidal shield, and that it is ventrally attached to the remaining part of the cranial cavity. The last feature prevents the placing of the forebrain hemispheres within the posterior part of the recess. Hence it may be supposed that, in *Porolepis* similarly as in *Latimeria*, the brain fitted wholly, or in its distinctly greater part, within the cavity of the otico-occipital. This is so probably in the genus *Eusthenopteron* too, where the anterior portion of the cranial cavity is extremely narrow. The corrugated, symmetrically bipartite anterior portion of the recess suggests that in *Porolepis* the pineal apparatus was paired.

The remaining antero-ventral part of the cranial cavity terminated at some distance behind the level of the external optic nerve openings (II), and thus did not protrude anteriorly beyond the level of the orbito-nasal wall. Hence, the ethmoidal part of the cranial cavity in *Porolepis* did not differ in this respect from that in *Eusthenopteron*.

Anteriorly the antero-ventral part of the cranial cavity passed into several broad olfactory canals (c.olf.). These run parallel to each other over a long distance and, after, medially attaining the anterior orbital corner, they diverge laterally to enter the postero-medial extremities of the nasal cavities. Hence the olfactory nerves in *Porolepis* behave analogously as in *Eusthenopteron*.

### c. Nasal cavity

In *Porolepis* the nasal cavity is relatively smaller than in *Eusthenopteron*. Fundamentally, however, this cavity is similar in both forms. Owing to the larger transversal dimensions of the ethmoidal region in *Porolepis*, the nasal cavity laterally extends farther, hence being relatively broader and shorter. In the centre of the antero-lateral compressed extremity occurs the slit-like fenestra exonarina anterior — fe.ena. Its front and bottom are rimmed by a thickening (pr.in.). In position it corresponds to the processus intermedius of *Eusthenopteron*, probably being its homologue. It does not, however, conspicuously project into the nasal cavity and does not cause its partition. This is most likely a consequence of the poorer development of the nasal organ in *Porolepis*, most particularly so of the greater thickness of the enchondral wall in the region of fenestra nasalis anterior, as compared with that in *Eusthenopteron*.

Downwards and laterally of the fenestra nasalis posterior communis (fe.npc.) the outer wall of the nasal cavity forms a step-like prominence or crest (cr.sbnr.), by Jarvik (1942) referred to as crista rostro-caudalis. This crest is formed by the medial border of the palatal lamina of the fronto-ethmoidal shield, transmitting the infraorbital (ioc.) canal, and by the thin

enchondral wall of the nasal cavity, repeating the configuration of the adjoining dermal element. The here considered crest separates the recesses of the posterior nasal tube recesses from the choanal recess. No supplementary recess is here present to lodge Jacobson's organ corresponding to the recessus lateralis in *Urodela*. In this connection there is no sound ground to homologize the subnarial crest (cr.sbnr.) with the crista rostro-caudalis. The former owes its origin to the penetration, progressively stronger backwards, of the nasal recess, directed to the fenestra exonarina posterior, into the partition which is thicker at its bottom owing to the presence there of the infraorbital canal.

Neither has it been possible to find in *Porolepis* an equivalent of the palatal process of Seydel. One of the parachoanal processes only could here be taken into consideration. The medial one (pr.pch.), however, lies medially to the choanal opening and, ought, therefore, to be excluded. The lateral one (pr.pch.l.) occupies a similar position in relation to the choanals as the palatal process of Seydel. However, in the absence of the lateral recess there is no fundamental criterion to homologize these two elements. A supposition that the subnarial crest (cr.sbnr.) corresponds to the crista rostro-caudalis (which has been shown to be incorrect), would place Seydel's palatal process along its prolongation, i.e. in another position than in *Urodela*.

The resulting conclusion is that *Porolepis* is not provided with equivalents of the crista rostro-caudalis and Seydel's palatal process, both so characteristic of *Urodela*, similarly as it lacks the lateral recess for Jacobson's organ. However, it would seem that the slight eminence in *Porolepis*, rimming from the front and partly from the bottom the fenestra nasalis anterior, is a homologue of the processus intermedius so strongly developed in Osteolepidae, and most particularly so in *Eusthenopteron*.

A large olfactory canal occurs in *Porolepis* in the postero-medial extremity of the nasal cavity. A smaller opening is present just in front of it on the roof of the nasal cavity. It most likely corresponds to the similarly placed canal in *Eusthenopteron* (Jarvik, 1942, fig. 57 A, C-E, c.cut.va.). Dorsally and laterally of the olfactory canal a large opening conducts to the nasal cavity of *Porolepis*, it lodged the N. ophthalmicus profundus and the accompanying vessels. As is suggested by grooves on specimen no. 4 and by the lack of additional lateral canals in the orbito-nasal wall of specimens nos. 1 and 4, the nerve and the vessels here were subdivided into the medial and lateral branches within the just mentioned opening (n.pr.), similarly as is the case in *Eusthenopteron*. The diameters of these grooves indicate that the nerve with its vessels did not fill up the whole lumen of the opening. Hence its considerable dimensions were not due to



any particularly strong development of the N. ophthalmicus profundus, but solely to the incomplete ossification of the area, on which the nerve with the accompanying vessels effected its penetration into the nasal cavity. An intermediary stage of this character in *Porolepis* and that in *Eusthenopteron foordii* will be observed in *Eusthenopteron wenjukowi*. At the place of penetration of the nervo-vascular complex the latter form (Jarvik, 1937, fig. 12, 13) displays a round depression with ossified bottom, pitted by smaller openings for the nerves and vessels. Supposing that the bottom of this depression (the orbito-nasal pit of Jarvik, 1937) remains unossified, the resultant large sized opening would fully correspond to the N. profundus canal in *Porolepis*.

As has been mentioned here above, the N. ophthalmicus lateralis likewise sometimes penetrates the nasal cavity by the c.pr. opening. Usually, however, this has its own foramen lying medially and dorsally to the c.pr. opening. A number of minute pits (cc.o.lat.), by Jarvik referred to as c.prt. (Jarvik, 1942, fig. 42 A, D, E), stretch from the N. ophthalmicus lateralis or, for lack of it, from the opening for N. ophthalmicus profundus; the pits doubtlessly transmitted to the neuromasts of supraorbital sensory canal twigs of the N. ophthalmicus lateralis, and not fibres of the N. ophthalmicus profundus.

A groove entering the c.cut.va? opening, already described and most likely corresponding to the c.cut<sub>2</sub>va? canalicule in *Eusthenopteron*, runs on the nasal cavity wall from the opening for the N. profundus, beneath the outlet of the N. ophthalmicus lateralis. Farther anteriorly, on the medial wall of the nasal cavity, there is a fair-sized opening, conducting to the canal, which pierces transversely the internasal wall and enters the opposite nasal cavity by a similar opening. This canal (c.in.trans.) gives off a number of branches in the interior of the internasal wall and apparently communicates with the medial cavities (for<sub>d</sub>m.) on the ventral face of the ethmoidal region. Should this be actually so it might be regarded as an equivalent of the naso-basal canal (c,n-b) in the genus *Eusthenopteron*.

On the back wall of the nasal cavity, midway between the olfactory nerve opening (c.olf.) and the fenestra nasalis posterior communis (fe.npc.), occurs a rather small opening of a canalicule, entering the orbito-ethmoidal wall medially to the processus apicalis area. This canalicule runs from the back and side, antero-medially, approaching the wall of the nasal cavity at a nearly right angle. Its course indicates that this canalicule could not have transmitted the twig of the N. ophthalmicus profundus. Its probable function will be discussed when describing nerves and vessels. In view of its uncertain status the present writer tentatively calls it the para-apical canal (c.pap.).

## d. System of nerves and vessels (fig. 5)

As has been shown in the beginning of this chapter, the vessel and nerve openings within the orbito-temporal region here fundamentally agree in respect to character and position with those occurring in *Eusthenopteron* and in representatives of the coelacanthids, e.g. *Latimeria*. Differences consist in the presence in *Porolepis* of a vena cerebralis anterior opening, which is missing in *Eusthenopteron*, and in the probable absence of an opening for the a.ophthalmica magna, which has been ascertained

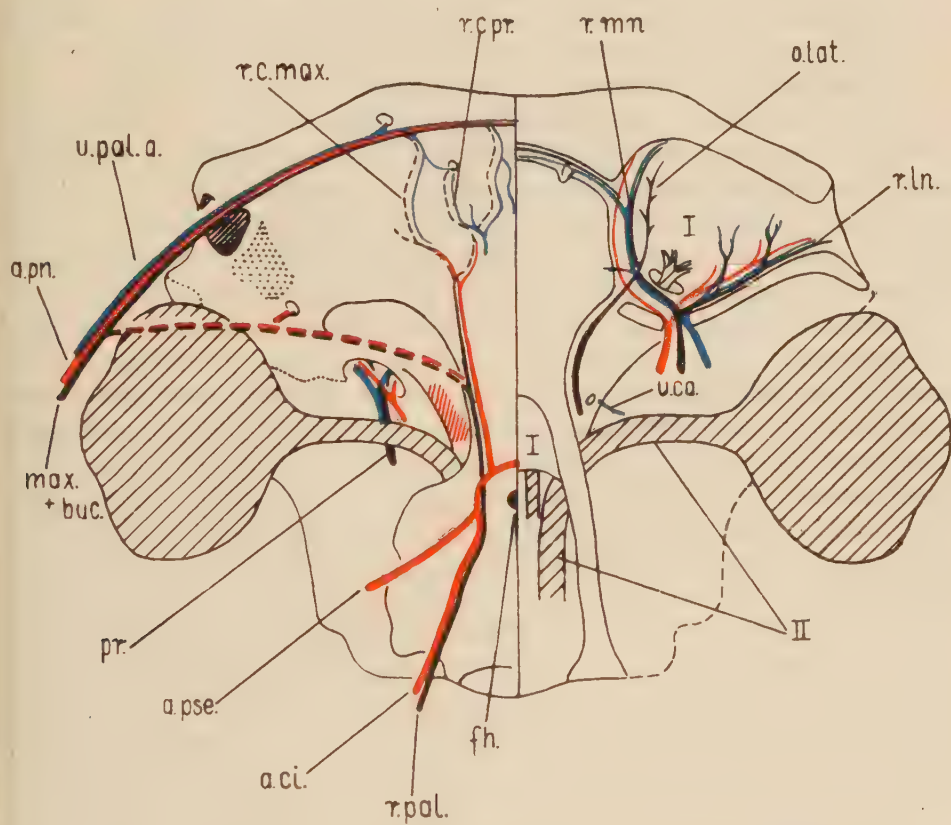


Fig. 5. — Outline sketch of the ethmosphenoid with attempted restoration of the nerves and vessels. On the left side — ethmosphenoid in ventral view, on the right — horizontal section of the same, in dorsal view

act. arteria carotis interna, a.pn. arteria palato-nasalis, a.pse. arteria pseudobranchialis efferens, fh. fenestra hypophyseos, max.+buc. N. maxillaris and r. buccalis lateralis VII (truncus infra-orbitalis?), o.lat. N. ophthalmicus lateralis, pr. N. ophthalmicus profundus, r.a.max. ramus communicans r. palatini VII cum N. maxillare, r.a.pr. ramus communicans r. palatini VII cum N. ophthalmico profundo, r.ln. ramus lateralis narium, r.mn. ramus medialis narium, r.pol. ramus palatinus VII, u.ca. vena cerebralis anterior, I N. olfactorius, II N. opticus.

in *Eusthenopteron*, also in *Nesides* among coelacanthids. It is in the basisphenoid region in *Porolepis* and, on the whole in holoptychiids only, that the course of vessels and nerves can be traced more fully than in other crossopterygian fishes. This is so in connection with the greater posterior width of the parasphenoid and with the formation by the basisphenoid of a wide support for this element. The groove (sulc.aci.) occurring here transmitted either the ramus palatinus VII alone, or, as seems more probable, this nerve together with a.carotis interna. Exact data on the vessel system of the now living crossopterygians fish *Latimeria* have not yet been published. On the description of the skeleton (Millet & Anthony, 1958) and the attached figures, it may be supposed that in the last named form the a.carotis interna stretched more laterally, piercing the skull more vertically. Transferring these conditions into *Porolepis*, a.carotis interna ought supposedly to be placed within the sulc.a.pse. groove. In the genus *Latimeria*, however, such a course of the a.carotis interna is associated with strong development of the subcranial muscles (muscles sous-céphaliques), which occupy in this form also a medial position in relation to a considerable part of the r.palatinus VII. It is hardly possible that these muscles, maybe analogously developed in *Eusthenopteron*, could have stretched in *Porolepis*, if present at all, farther to the front, beyond the level of the basipterygoid process. The lingual processes on the basisphenoid may possibly have been its place of attachment. In connection with the poorer development of the subcranial muscles in *Porolepis* a.carotis interna and r.palatinus VII must have been directed more medially. Hence it seems more probable that both the just mentioned nerve and the accompanying vessel were transmitted by the sulc.aci.groove, while the sulc.a.pse. groove would in that case transmit a.pseudobranchialis efferens. Farther to the front from the junction of the vessels, a twig of a.palatina probably branched off from a.carotis interna. It must have run along the r.palatinus VII to the medial cavity of the ethmoidal region, anastomosing with the artery accompanying the N.maxillaris. The a.carotis interna united with the corresponding vessel of the opposite side and entered the cranial cavity in front of the hypophysial opening.

As has been mentioned here above, the N.opthalmicus lateralis penetrates the nasal cavity either by means of an independent opening, dorso-laterally of the N.opthalmicus profundus, or together with the last named nerve. Thereafter it runs on the medial part of the nasal cavity roof, giving branches into the supraorbital canal.

N.opthalmicus profundus enters the nasal cavity by a large opening, laterally and dorsally to the entrance of the N.olfactorius, with the accompanying veins and arteries, which later on ramify in agreement with the



branches of the nerve. Already during their course within the orbito-nasal wall the nerve and vessels give off lateral twigs, stretching laterally on the posterior wall of the nasal cavity (sulc.ln.), to supply the lateral portions of that wall, as well as medial ramifications, stretching on the dorso-medial wall of the nasal cavity and piercing the internasal wall. Vessels of the two sides were united within the internasal wall. Twigs of the N.ophthalmicus profundus may possibly have made their way to the ventral side of the ethmoidal region, by means of the opening at the bottom of the medial cavity, uniting with the terminations of r.palatinus VII. Their behaviour would thus have been analogous to that of twigs of r.medialis narium in *Eusthenopteron*, as reconstructed by Jarvik. The slightly different direction of their course is connected with dissimilarities in the mutual position of the nasal cavity and the medial cavities; in *Eusthenopteron* those are adjacent vertically, while in *Porolepis* horizontally.

Hence, though the course of the terminal minute twigs of the N.ophthalmicus profundus has not been quite certainly determined, it is doubtless that the larger branches (rr.mediales et laterales narium) behave analogously in *Eusthenopteron* and in *Porolepis*.

Jarvik (1942) distinguishes the following branches of the N.maxillaris in *Eusthenopteron*: 1) the ramus infraorbitalis, entering the nasal cavity through the "fenestra endonarina posterior" (this is the opening here identified as corresponding with the dorsal part of the fenestra nasalis posterior communis in *Porolepis*); 2) the postchoanal anastomose uniting within the anterior portion of the orbita with ramus palatinus VII; 3) the ramus palato-nasalis lying laterally to the choana in the canal along the medio-ventral border of the fronto-ethmoidal shield and running to the prenasal pits; it gives off branches to the maxillary and premaxillary teeth and, within the prenasal pits, uniting with the terminal twigs of ramus palatinus VII; 4) the rami cutanei.

Identical branching may have occurred in *Porolepis*. The ramus infraorbitalis may have thus entered the nasal cavity in the dorsal part of the fenestra nasalis posterior communis; behind the orbito-nasal wall there may have occurred the joining with ramus palatinus VII, through the intermediary of ramus communicans; the rami cutanei may have branched in the soft tissues of the suborbital region. The course taken by these ramifications and even their very presence is equally hypothetical in *Porolepis* as in *Eusthenopteron*, since in neither form did they leave any traces in the form of an osseous canal. The ramus communicans only in *Eusthenopteron* runs in its own groove on the dermopalatine, and farther on the boundary between the latter and the autopalatine. The corresponding bone elements in *Porolepis* have not yet been studied.

The normal development of N.maxillaris in *Porolepis* and the similar behaviour of its twigs in *Porolepis* and in *Eusthenopteron* are suggested by the presence of a groove, occasionally closed up into a canal. Its function was doubtlessly that of transmitting the ramus palato-nasalis, which is a twig of the N.maxillaris, or perhaps the truncus infraorbitalis, i.e. the nerve trunk formed together by the tissues of N.maxillaris and buccalis lateralis VII. The fibres of the N.maxillaris penetrated into the ethmoidal region ventrally to the parachoanal lateral process (pr.pch.l.), that is laterally to the choana. Farther on they stretched in a groove, or a canal, along the inner border of the ventral palatal lamina of the fronto-ethmoidal shield (sulc.marg.). Near the antero-median corner of the vomeral area (ar.Vo.) and, at the same time, near the antero-lateral corner of the medial depression, the nerve branch entered the opening between the premaxillary bone and the adjoining enchondral part. Another branch entered the medial depression probably joining with the terminal twigs of r.palatinus VII. Corresponding vessels must have certainly run along with the just described branch of N.maxillaris. Hence there is no sound evidence to suppose that N.maxillaris played a more limited part in the nervous system of the ethmoidal region in *Porolepis*, as compared with that in *Eusthenopteron*.

Ramus palatinus VII was probably transmitted in the groove sulc.aci. and farther on along the border of the parasphenoid. Upon piercing the vomer of the suitable side, it entered the medial depression on the ventral face of the ethmoidal region. Here the terminal twigs could have met the twigs of N.opthalmicus profundus and ramus palato-nasalis V. Apparently, part of the fibres of ramus palatinus VII entered the medial cavity (fov<sub>m</sub>.) directly beneath the anterolateral corner of the parasphenoid, without passing through the canal in the vomer. This was also probably the way followed by the artery and the vein accompanying that nerve. Before attaining the level of the orbito-nasal wall, r.palatinus VII may have anastomosed transversally with the N.maxillaris.

No particular canal is traceable in *Porolepis* for the ramus buccalis VII. The presence of an "orbito-rostral passage", described by Jarvik (1942), could not be ascertained. The para-apical canalicule (c.pap.), whose position may possibly correspond to that of the posterior part of the "orbito-rostral passage", is differently directed. On piercing the orbito-ethmoidal wall, it stretches medially to enter vertically the nasal cavity. There is nothing to suggest its farther position at the bottom of the nasal cavity, or its union with the groove bounded by the crista subnarina and crista orbitorostralis (cr.or.), postero-laterally stretching to the choana. This behaviour excludes the placement of twigs of the N.profundus and r.buccalis lateralis within the para-apical canal. This might have rather

transmitted a vessel branched off from the hypothetical arterial anastomosis, similarly as in *Polypterus*; or from a vein anastomosis, as in some amphibians; or perhaps the para-apical canal was connected with the twig of the N.maxillaris or that of ramus communicans N.maxillare cum N.palatino VII. Hence r. buccalis lateralis may only have stretched laterally of the choana, with the twig of the N.maxillaris, together possibly to form a common trunk, the tr.infraorbitalis. It should be noted here that the presence of a separate canal for r.buccalis VII is equally hypothetical in the case of *Eusthenopteron*. As has been demonstrated by tables, attached to Jarvik's monograph (1942, p. 11-13), the part supposedly corresponding to the position of r.buccalis is without a canal having its own wall, such as is encountered even in ducts for relatively small twigs, e.g. the terminal twigs of ramus medialis narium.

#### e. *Parasphenoid*

A cast of the anterior portion of the parasphenoid only is preserved in the Daleszyce material. According to a pattern typical of the genus *Porolepis*, it is relatively narrow and provided with a longitudinal crest, bearing a row of denticles. On the shape of the basisphenoid it may be supposed that the posterior portion of the parasphenoid did not to any great extent differ from that common in all holoptychioids. It must have been broad with an arcuate transversal groove stretching on the surface. The central course of the groove probably corresponded to the position of the hypophyseal opening. In all the holoptychioids this groove runs along that part of the parasphenoid which rests on the ventral and distal face of the basipterygoid process, and hence laterally enters the cavity lying behind the junction of the palatoquadrate with the skull, that is the spiracular cavity. If we recognize the connection of this groove with the gill-slits, it must be called spiracular. The hypothetical prespiracular groove would then stretch to the slit between the mandibular and the premandibular arches, and would open up not farther than just in front of the basipterygoid process. The course followed by the supposed prespiracular groove would have to coincide with the boundary between the area of the derivatives of the mandibular arch and that of the derivatives of the premandibular arch. As results from the diagram drawing given by Jarvik (1954, fig. 39 C), the former is overlapped by the parasphenoid, which thus delimits the boundary of the area of the derivatives of the mandibular arch. The vomers occupy and delimit the area of derivatives of the premandibular arch. It is, therefore, hardly probable that the hypothetical prespiracular groove could transect the surface of the parasphenoid. Its position on the boundary between the parasphenoid and the vomers is much more likely.



Since the groove occurring on the parasphenoid of holoptychioids is the spiracular groove, it must be consequently recognized that, in what the gill-slits and the gill-arches are concerned, the parasphenoid of Crossopterygii has attained the same evolutionary stage as Palaeoniscidae and the Arthrodira (or at least the Brachythoraci).

Another problem is that concerning the homology of the various lateral processes on the parasphenoids of the different fish lineages. Independently of their shape and of the fact whether they are the so-called anterior ascending processes, or posterior ascending processes, or maybe both, all of them are invariably connected with the mucuous area behind the mandibular arch and with its derivatives included in the skull, that is belonging to the hyoid arch area. Thus, without taking into account the number of the component elements, the just mentioned processes would be mutually homologous, independently of their shape. The only exceptions here would be such cases, as e.g. in *Polypterus* (Jarvik, 1954), where elements belonging to other gill-arches are included into these processes. Considering that all the attempts to trace adequate criteria for homologizing the anterior and posterior ascending processes in various fishes have, so far, proved a failure, the diagnostic value of the shape of parasphenoidal processes, as well as their presence or absence, should not be over-estimated, when dealing with phyletic relations. That heed should be exercised in this respect is moreover suggested by the secondary character of the shape of these processes, i.e. that their appearance is controlled by the shape of the cranial base. Seemingly there is a correlation, though not an absolute one, between the degree of development of the lateral and ascending processes in the parasphenoid, and the width and degree of flattening of the cranial base. Thus in Arctolepida, with the base exceptionally broad and flat, the parasphenoid is devoid of all processes. The same applies to dipnoids, who have the cranial base considerably broader and more flat than that in actinopterygians and crossopterygians. Incipient lateral processes are observable on the parasphenoid of the Brachythoraci, in which the ethmosphe-noidal region of the cranial base is notably narrower than in Arctolepida. Moreover, the development and general appearance of the parasphenoidal processes in crossopterygians are apparently affected by the behaviour of the intercranial slit, as well as by the presence and behaviour of the subcranial muscles.

#### f. Lower jaw

The posterior part of the lower jaw in the genus *Porolepis* is unknown. However, close structural similarities of other skeletal elements suggest that it did not differ from that common in the genus *Glyptolepis*. In the latter (Gross, 1941), a number of canals arise in the distal portion of the

lower jaw. One of the canals starts as an opening between the articular and the supra-angular, near to the dorsal face and then penetrates the infra-dental series (angularis, splenialis), stretching to the front of the jaw and opening up near the border of splenialis 1. In *Porolepis* it occurs on the level of the posterior margin of the symphyseal area of the mentomandibular. This canal, by Gross (1941) referred to as "c.m.", corresponds, in agreement with that author's interpretation, to the sensory line canal — canalis mandibularis, provided with nerves by the r. mandibularis externus VII.

The outlet of the canal, piercing the articular (canalis articularis, c.art.) and entering the Meckelian cavity, occurs near the ventral margin, below the surface for the articular, somewhat more medially. This canal probably transmitted the r.mandibularis internus VII (= chorda tympani) since in this region it is the only one answering the required conditions. Above the posterior outlet of the canalis articularis, on the margin of the prearticular, Gross ascertained in *Glyptolepis* the beginning of a canalicule (canalis prearticularis, c.pra.), running anteriorly between the prearticular and the articular. That author states that he did not discover the continuation of that canal nor its outlet into the Meckelian cavity. In view of the fairly large dimensions of that canalicule, it is hardly probable that it only transmitted the nutritive vessels for a small portion of the Meckelian bone constituting the articular, or for the prearticular. This is, however, not impossible. It is not out of the question that the lack of its prolongation may be due to the unsatisfactory state of preservation of the studied specimen. In all probability, a canal, by Gross marked with the symbol "c.z." and encountered in *Glyptolepis*, *Porolepis* and elsewhere, e.g. in *Panderichthys*, constitutes the prolongation of that canal. In *Laccognathus* it seems to reach to the symphysis. It is possible that in *Glyptolepis* and in *Porolepis* it opens up anteriorly by a foramen, by Gross marked with the symbol "ca.". This foramen occurs on the boundary between the prearticular, the mentomandibular and the splenial, approximatively on the same level as the mandibular line canal (c.m.), but somewhat more dorsally. In *Panderichthys* this canal opens up on the medial (internal) surface of the jaw, on the level of the procoronoid. At that point two grooves separate from it; one of them runs towards the dental pit on the procoronoid, while another enters, together with the above considered canal "ca.", into the depression in front of the procoronoid (fov<sub>d</sub>l), by Gross marked with the symbol Pg<sub>1</sub>. This depression most likely lodged an important venous sinus, which crossed by means of a wide outlet the antero-lateral procoronoid process on the boundary between its tooth-bearing and toothless portions. Then it passes into a groove bounding the dental and the coronoids. In *Panderichthys* this groove is strongly deve-

loped. It communicates there with the intercoronoid depression (probably lodging the venous sinuses), this time, however, by means of a tunnel beneath the lateral processes of the adjacent coronoids. Numerous canalicules enter the groove penetrating the interior of the jaw. In *Panderichthys* two such openings are to be seen just behind the grasping teeth or behind their cavities on the boundary of the widened up part of the dentale and the antero-lateral procoronoid process. Here the groove curves medially (ventrally) and gives off branches directed anteriorly, while others stretch ventrally backwards. That whole net-work, including the "c.z." canal of Gross and probably the c.prearticularis canal, most certainly lodged vessels and venous sinuses. In holoptychioids and among them in *Porolepis*, the net of veins and corresponding canals was less developed, but, on the whole, in a similar fashion. This applies particularly to vessels and marginal canals between the dental and the coronoids, on the outer surface of all specimens, described in detail in the foregoing chapter; this applies also to the presence of the groove along the medial border of the dentale, between the latter and the Meckelian bone, discernible in specimen no. 8 after the removal of coronoids. Transversal grooves stretch from the just mentioned one; those are directed medially across the intercoronoid depressions and seemingly penetrate below the prearticular. Above such a transversal groove the lateral processes of the coronoid and the intercoronoid span in a fashion similar to that in *Panderichthys*. The anterior transversal groove runs in front of the procoronoid depression and is not covered up. The vessel transmitted by it probably united with that passing through the soft tissues along the medial ventral margin of the Meckelian bone. Laterally, the just mentioned groove gives off a branch, passing to the front, below the antero-lateral procoronoid process. The net-work of minute twigs branching off the transversal groove covers up the surface lying at the front, causing its roughness.

Besides those just mentioned, the r.mandibularis V nerve with the accompanying vessels most probably also penetrated the lower jaw through the Meckelian cavity. Within this cavity that nerve very likely forked into two major twigs, the r.alveolaris inferior, i.e. the ramus mandibularis V lateralis, and the r.mandibularis medialis, corresponding to the r.mylohyoideus, while its terminal end was the equivalent of the r.lingualis in higher vertebrates. The first mentioned of them penetrated between the dentale and the Meckelian bone, running along the a.alveolaris inferior artery and the v.alveolaris inferior s.mandibularis lateralis vein. In *Panderichthys* this vascular bundle finds its equivalent in a canal, by Gross named "c.d."; in *Porolepis* (Holoptychiidae) its corresponding elements are the just mentioned groove on the boundary of the dental, the Meckelian



bones and the coronoids. The other one of the here mentioned nerve branches extended together with a mandibularis medialis s.interna (a.mylohyoidea of higher vertebrates) and v.mandibularis superior (Hochstetter) s.meckeli (Nilsson, 1943). Passing through the Meckelian cavity this bundle stretches to the foramen Meckeli (s.meckelianum anterior) f.mylohyoideus anterior (by Gross marked with the symbol "c.b."), beyond which the terminal twigs pass to the outside. During its course in the Meckelian cavity this nerve, and the accompanying vessels probably too, give off branches to the successive coronoids, directed towards the symphysis.

### CONCLUSIONS

Very close agreement of the ethmoidal region in *Porolepis* and *Eusthenopteron* are suggested by the here described materials from the Lower Devonian of Daleszyce. The existing differences mainly refer to proportions. In *Eusthenopteron* the front of the snout has undergone elongation and constriction; in *Porolepis* it has been shortened and widened out. In the latter form this, to a large extent, means the retention of primitive characters. The just mentioned differences concerning proportions, and others occurring within the ethmoidal region of both forms, are connected mainly with the degree of development of the nasal tract and with the different specialization of dentition. *Porolepis* realize a low stage of evolution of the nasal apparatus. The nasal cavities and the choana are small, the internasal wall broad, the fenestra nasalis posterior externa has persisted. To a large extent these characters likewise refer to ancestors of the genus *Eusthenopteron*, i.e. Osteolepidae (comp. Jarvik, 1942, fig. 62 B, *Thursius?*). In them the striking features are: the shortness and width of the ethmoidal region; small, widely spaced vomers; relatively short and broad parasphenoid; presence of a stout support for the parasphenoid. The far spacing of vomers and the appearance of the nasal openings, the widely spaced nasal cavities and the choanal openings — indicate considerable width of the internasal wall. In what dentition is concerned, the grasping teeth on the dentale in *Eusthenopteron* are by Jarvik said to have been lost. In this connection the pits for these teeth on the ventral surface of the ethmoidal region are vestigial. In *Porolepis*, however, they have become peculiarly specialized. The nerve and vascular systems in *Porolepis* agree perfectly with that in *Eusthenopteron*, particularly so in what the major branches are concerned. In *Eusthenopteron*, similarly as in other Osteolepoidei, the posterior external nostrils disappear in consequence of the wide communication between the oral and the nasal cavities provided by choanae.

The close similarities existing between *Eusthenopteron* and *Porolepis* suggest their relatively close relationship. The differences between them

do not, in the writer's opinion, exceed those fitting within the rank of superfamilies. Hence the here discussed forms ought to be placed within two superfamilies: Osteolepioidei and Holoptychioidei, instead of being referred to two distinct orders, the Osteolepiformes and the Porolepiformes (s. Holoptychiiformes of Berg).

The studies of Jarvik (1942) and Ørvig (1957) have shown the closest resemblances between *Porolepis* on the one hand, and *Glyptolepis* and *Holoptychius* on the other. In fact there is reasonable ground to postulate direct relationship between these three genera, which represent three successive morphologic stages of one lineage. Differences refer mainly to varying extent of the reduction of the dentine-enamel coating on the dermal bones and scales, and proportions. These differences do not surpass the rank of subfamilies. In systematics this would mean the assignment of the three just mentioned genera to the same family of Holoptychiidae. This family would comprise the subfamily of Porolepinae, characterized by the presence of cosmine on the dermal bones and scales, as well as that of Holoptychiinae, where the dentine coating has suffered disintegration in a varying degree, or has even completely disappeared. *Glyptolepis*, *Laccognathus* (differing from the former in the presence of peculiar cavities on the lower jaw), also *Holoptychius* and perhaps *Hamodus* — would thus all be referable to the Holoptychiinae. The Porolepinae at present seem to be monotypical.

Remains of the genus *Porolepis*, represented by scales from erratic boulders, were first described by Kade in 1858 as *Gyroptychius posnanien-sis* and *Gyrolepis posnaniensis*. Woodward, when describing scales of this form discovered in Spitsbergen, ascertained the identity of the two forms distinguished by Kade, and separated them from the genus *Gyroptychius* by establishing the new genus of *Porolepis* (1891). Later on remains of the genus *Porolepis*, chiefly in the form of scales, have been recorded from the Upper Siegenian and Lower Coblentzian of the Rhine Province (Gross, 1933), from the Lower Devonian of Siberia, the Middle Devonian of the Ural (Obručev, 1957) and from the Baltic countries (Gross, 1950).

In spite of frequent occurrence and wide generic distribution and though it has been known for one hundred years, this really existing genus does not contain any well defined species. Kade's *P. posnaniensis* and Obručev's *P. uralensis* are identified on a few scales, that is on elements which cannot be considered as diagnostic for species. The species *P. siegensis* and *P. hefteri* have been established by Gross on fragments of the shoulder girdle. It is possible that *Porolepis siegensis* is merely a less complete fragment of the shoulder girdle, belonging to *P. hefteri*, if not referable to another genus. The Spitsbergen species *P. spitsbergensis*, *P. elongata* and *P. brevis*, subsequently established by Jarvik (1942), are not comparable

with the above named forms, being based on differences of proportions in the ethmoidal region. In view of the nature of differences between these three tentatively established species, their precise definition requires statistical methods, based on ample undeformed material. It is here possible that differences of proportions are due to individual variations, connected with age and sex, as well as to post-mortem deformations. This is suggested by similar variation range in material from the Holy Cross Mountains.

In this state of conditions, particularly for lack of more detailed data on the Middle Devonian form from the Baltic countries, by Gross postulated to be *P. posnaniensis*, typical of the genus, every attempt to determine the specific position of *Porolepis* from the Polish Devonian, is fruitless. Therefore, the here described specimens are by the present writer tentatively referred to the group of the forms including *Porolepis posnaniensis*. This is moreover suggested by the possibility of the occurrence of more than one species within the wide range of distribution, and the long lapse of time over which the genus *Porolepis* has been recorded. For example, very probably the Rhine and Polish forms are two distinct species (or subspecies) since, as is shown by Gross, in the former the prearticular is coated by cosmene, while in specimens from the Holy Cross Mountains, regardless of dimensions, it is strewed with shagreen denticles. Since the disintegration of the uniform dentine coating in rhipidists is of secondary character, it may be supposed that our form, displaying a more advanced evolutionary stage, if not identical with the Middle Devonian forms, will in any case be nearer to them, than are the Rhine specimens.

Independently of the specific position of the representative of the genus *Porolepis* from the Devonian of Poland, general conclusions do not lose any of their significance since they concern superspecific structural features, characteristic of the whole stock of the *Holoptychioidei* v. „*Porolepiformes*”.

Hence we may reasonably infer that the *Holoptychioidei* and *Osteolepιοidei* are closely allied superfamilies, whose differentiation dates back to the early stage of development of the choanae in primitive *Rhipidistia*. At this evolutionary stage the choanae did not, most probably, fulfil any important function in the respiration process of atmospheric oxygen.

The slight dimensions of the choanal openings in *Holoptychioidei* would rather suggest that in these fishes the nasal ducts had not yet been included into the respiratory system. The poor development of the nasal apparatus, that of choanae particularly so, together with the peculiar specialization of dentition and the skeletal structure of the pectoral fins, introduce doubts as to the *Holoptychioidei* being the ancestors of any tetrapods. Moreover, the *Porolepis* material from Daleszyce has proved that *Holoptychioidei* are not provided with such structures as *crista rostro-caudalis*, *processus pala-*



talis Seydeli, recessus lateralis for Jacobson's organ, nor a well developed intermaxillary gland. N. maxillaris is equally important in the nerve system of the ethmoidal region as N. profundus. The latter is not particularly well developed. R. buccalis lateralis runs laterally of the choana. Hence there is no such element that would be a characteristic link of the Holoptychioidei with *Urodela*. Thus, the problem of the supposed polyphyletic origin of amphibians, if not completely eliminated, must at least be restricted to ascertaining that ancestors of all tetrapods are to be sought for among forms, tentatively grouped in the family of Rhizodontidae, while Holoptychioidei should be regarded as a blind branch of the stock of Rhipidistia.

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JULIAN KULCZYCKI

## POROLEPIS (CROSSOPTERYGII) Z DOLNEGO DEWONU GÓR ŚWIĘTOKRZYSKICH

### *Streszczenie*

Wyniki badania szczątków *Porolepis* z dolnego dewonu Gór Świętokrzyskich opisanych w tej pracy prowadzą do wniosku, że pod względem budowy ethmosphenoideum rodzaj ten wykazuje daleko idące podobieństwo z rodzajem *Eusthenopteron*. Wyraża się ono: 1) w homologii zagłębień (fov<sub>am</sub>.) na brzusznej powierzchni okolicy nosowej; 2) w obecności u obu form synchronotycznego połączenia między processus apicalis palatoquadrati i okolicą nosową ethmosphenoideum; 3) w braku nosowego odcinka jamy czaszkowej; 4) w takim samym przebiegu, sposobie rozgałęziania się i stopniu rozwoju nerwów N. ophthalmicus profundus, N. maxillaris, r. palatinus VII, r. buccalis VII i towarzyszących im naczyń.

Ethmosphenoideum rodzaju *Porolepis* różni się od odpowiedniego elementu u *Eusthenopteron*: a) niewielkimi rozmiarami i b) znacznym oddaleniem od siebie jam nosowych, a w związku z tym c) dużą szerokością przegrody międzynosowej; d) małymi choanami; e) zachowaniem stosunkowo długiego tylnego kanału nosowego i brakiem podziału jego na kanały wtórne; f) brakiem, lub słabym stopniem rozwoju wyrostka proc. intermedius; g) zachowaniem tylnego otworu nosowego zewnętrznego; h) obecnością w jamie nosowej grzebienia związanego z przebiegiem kanału podoczno-

dołowego; i) silnym rozwojem jam przyśrodkowych; j) niekompletnym skostnieniem ściany oczodołowo-nosowej w miejscu wnikięcia *N. profundus*; k) dużą szerokością i ogólnymi kształtami basisphenoideum (oraz tylnej części parasphenoideum); l) zachowaniem się *v. cerebialis anterior*.

Cechy *a*, *b*, *c*, a także *f* oraz *k*, które należy uważać za pierwotne, spotyka się również u *Osteolepidae*. Punkty *d*, *e*, *l* dotyczą cech prymitywnych, właściwych zapewne wszystkim przodkom *Rhipidistia* i zachowanych przez *Porolepis* i bliskie mu formy, a utraconych przez *Osteolepidae* i *Rhizodontidae*. Wreszcie punkt *i* odnosi się do swoistej specjalizacji *Porolepis* i jemu podobnych.

Przyjmując powyższą ocenę różnic i biorąc pod uwagę znaczne podobieństwo (punkty 1-4) między *Porolepis* i *Eusthenopteron* — autor stoi na stanowisku naturalności szczepu *Rhipidistia*.

Obecność u *Porolepis* grzebienia homologicznego z *crista rostro-caudalis* i podniebiennego wyrostka Seydela, charakterystycznych dla płazów ogoniastych, a nie występujących u innych kręgowców czworonożnych, okazała się co najmniej problematyczna. Jednocześnie z przyjęciem nowej interpretacji szczegółów morfologicznych rodzaju *Porolepis*, oznaczonych nazwami *crista rostro-caudalis*, *processus palatalis* Seydela i *cavum internasale*, oraz ze stwierdzeniem podobnego zachowania się nerwów i naczyń u *Porolepis* i *Osteolepioidei* (= *Osteolepiformes* Jarvik, 1942; Berg, 1950; Bertin & Arambourg, w Grassé, 1958), znikają rzekome podobieństwa między *Holoptychioidei* (= *Porolepiformes* Jarvik, 1942; Bertin & Arambourg, 1958; = *Holoptychiiformes*, Berg, 1950) i *Urodela*. W konsekwencji, przypuszczenie o polifiletycznym pochodzeniu płazów — o ile nie powinno być całkowicie odrzucone — musi ulec znacznemu ograniczeniu przez uznanie, że przodkowie czworonogów wywodzą się nie z dwóch odrębnych rzędów, lecz co najwyżej z członków jednej rodziny ryb kwastopłetwych, a mianowicie z *Rhizodontidae*.

Co się tyczy nieparzystej kości skórnej podstawy czaszki — *parasphenoideum*, to znajdujący się na niej rowek otwiera się z tyłu za wyrostkiem *processus basiptyergoideus*, czyli do jamy spirakularnej. Jeżeli więc związek tego rowka ze szczelinami skrzelowymi jest rzeczą istotną, musi być uznany za spirakularny i w konsekwencji stwierdzić musimy, że *parasphenoideum* u *Crossopterygii*, *Palaeoniscidae* i *Placodermi* (a przynajmniej u *Brachythoraci*) znajduje się na jednym i tym samym stadium rozwojowym rozpatrywanego elementu.

#### OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 70)

Tarcza czołowo-nosowa i *ethmosphenoideum*, od strony brzusznej; z lewej strony — bez *basisphenoideum* i tylnej części *parasphenoideum* (wg okazu no. 1), z prawej — przekrój na poziomie kanałów nerwów węchowych i jam nosowych.

Fig. 2 (p. 71)

Rysunek diagramatyczny okolicy wspólnego tylnego otworu nosowego (*fe.enpc.*).



Fig. 3 (p. 75)

Одlew prawej jamy nosowej od strony grzbietowej (A) i brzusznej (B).

Fig. 4 (p. 77)

Fragment szczęki dolnej (z lateksowego odlewu okazu no. 7); w.nat.

Fig. 5 (p. 89)

Rekonstrukcja przebiegu niektórych naczyń i nerwów u *Porolepis*. Z lewej strony — ethmosphenoideum od strony brzusznej, z prawej — od strony grzbietowej, po usunięciu sklepienia.

## Pl. I

Odciski etmosfenoidów od strony grzbietowej: A okaz no. 1, B okaz no. 2;  $\times 2$ .

## Pl. II

A odlew lateksowy basisphenoideum, od strony brzusznej, w.nat.; B odlew lateksowy etmosfenoidu (okaz no. 1), od strony brzusznej,  $\times 1,5$ .

## Pl. III

Okaz no. 3: A okolica nosowa, od tyłu; B to samo, po usunięciu odlewu lewej jamy nosowej; C odlew lateksowy od strony brzusznej;  $\times 1,5$ .

## Pl. IV

Одlew lateksowy okazu no. 4: A strona brzuszna, B od tyłu;  $\times 1,5$ .

## Pl. V

Dolne szczęki: A okaz no. 7  $\times 0,5$ ; B okaz no. 8,  $\times 1,5$ ; B' odlew lateksowy tegoż okazu; C, D odlewy lateksowe okazów no. 9 i 10,  $\times 1,5$ .

## Pl. VI

Одлеwy lateksowe łusek (fig. 1-15), zębów (fig. 18-23) i dwóch nieoznaczalnych fragmentów kostnych (fig. 16, 17) rodzaju *Porolepis*; w. nat.

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ЮЛИАН КУЛЬЧИЦКИ

POROLEPIS (CROSSOPTERYGII) ИЗ НИЖНЕГО ДЕВОНА  
СВЕНТОКРЖИСКИХ ГОР

## Резюме

Изучение остатков *Porolepis* из нижнего девона Свентокржиских Гор, описанных в настоящей работе приводит к заключению, что по строению этмосфеноида род этот обнаруживает далеко идущее сходство с *Eusthenopteron*. Выражено оно: 1) в гомологии углубления (fovam. = „cavum internasale” = „prenasal pits”) на брюшной поверхности носовой области; 2) в наличии у обоих форм синхондротического сочленения между processus apicalis palatoquadrati и обонятельной областью этмосфеноида; 3) в отсутствии этмоидального участка черепной полости; 4) в таком же расположении нервов

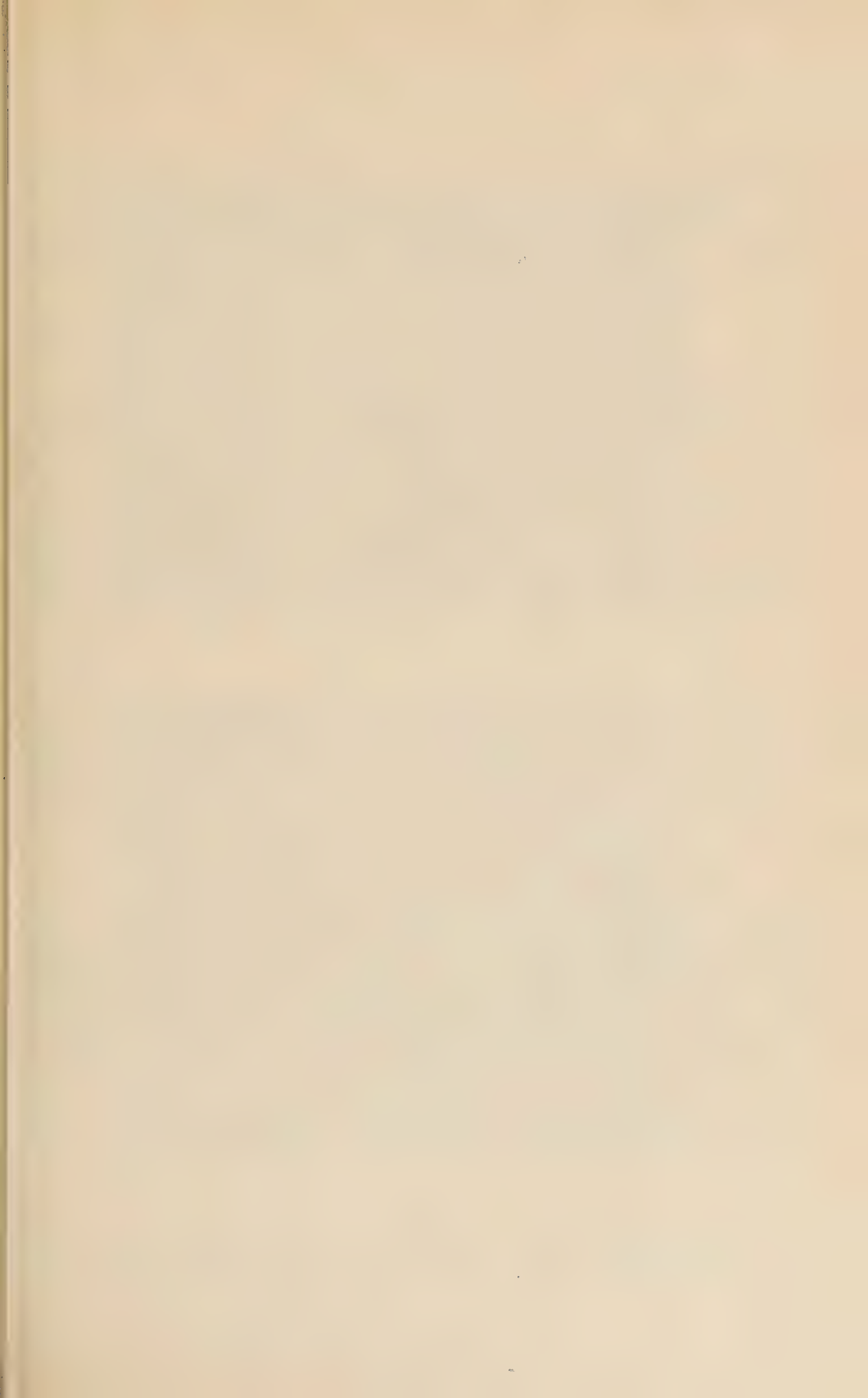
(*N. ophthalmicus profundus*, *N. maxillaris*, *r. palatinus VII*, *r. buccalis VII*) и сопутствующих сосудов.

Этмосфеноид рода *Porolepis* отличается от свойственного роду *Eusthenopteron*: а) небольшой величиной и б) значительным удалением друг от друга носовых полостей, а в связи с этим и в) большой шириной межносовой перегородки; г) небольшой величиной хоан; д) сохранением относительно длинного заднего носового канала и отсутствием подразделения его на вторичные каналы; е) слабо развитым отростком *processus intermedius*; ж) сохранением заднего наружного носового отверстия; з) присутствием в носовой яме гребня *crista subnarina*, связанного с прохождением подглазничного сейсмочувствительного канала и заднего носового канала; и) сильно развитыми углублениями *fovea*; к) неполным окостенением глазнично-носовой стенки в месте входа *N. profundus*; л) большей шириной и общей формой базисфеноида (а также задней части соседствующего парасфеноида); м) сохранением *v. cerebralis anterior*.

Признаки а, б, в, а частично и ж, л, которые следует считать примитивными, встречаем тоже у *Osteolepidae*. Также примитивными являются признаки г, д, м, которые были повидимому свойственны предкам всех *Rhipidistia* и сохранились у *Porolepis*, но исчезли у большинства *Osteolepidae* и *Rhizodontidae*. Наконец признак и связан со своеобразной специализацией семейства.

Автор имеет возможность убедиться, что у *Porolepis* нет ни *recessus lateralis* для яacobsonового органа, ни каких нибудь образований, которые могли бы соответствовать *processus palatalis Seydela*. Гомология же гребня *crista subnarina* с *crista rostrum-caudalis*, также как и наличие уже у кистеперых рыб высоко дифференцированной межчелюстной железы, является крайне сомнительной. Из выше изложенного явствует, что между *Holoptychiidae* и хвостатыми амфибиями нет никакого особенного сходства. Если даже считать приведенные факты недостаточными для полного опровержения гипотезы полифилетического происхождения амфибий, так во всяком случае заставляют ограничить предков всех тетрапод до одного семейства — *Rhizodontidae*.

Что касается непарной покровной кости основания черепа — парасфеноида, так находящийся на нем желобок открывается позади *processus basiptyergoideus*, т. е. в полость спиракулярную. Ввиду этого, если считать существенными соотношения с жаберными щелями, так упомянутый желобок следует звать спиракулярным. Если это верно, так парасфеноиды кистеперых палеонисцид и ланцырных рыб (по крайней мере *Brachythoraci*) находились бы на одной и той же стадии развития рассматриваемого элемента.





## Pl. I

Imprints of ethmosphenoids in dorsal view: *A* specimen no. 1, *B* specimen no. 2;  $\times 2$   
*c.cut.va?* canal, probably for cutaneous vessels, *c.olf.* canalis olfactorius, *c.pr.* canal  
 for *N. ophthalmicus profundus*, *cav.cr.* cavum cranii, *cav.nas.* nasal cavity, *fov<sub>d</sub>m.* me-  
 dial depression, *la.pal.* palatal lamina of the fronto-ethmoidal shield, *rec.pin.* recessus  
 pinealis, *sulc.o.lat.* groove for *N. ophthalmicus lateralis*, *te.orb.* tectum orbitae, *x* trace  
 of damage.

## Pl. II

*A* latex cast of basisphenoid, in ventral view; nat.size.

*B* latex cast of ethmosphenoid (specimen no. 1), in ventral view; 1.5

*ar.mm.obl.* area for oblique eye muscles, *ar.Vo.* vomeral area, *c.pap.* canalis paraapi-  
 calis, *art<sub>1</sub>m* autopalatine articular area, *c.pr.* canal for *N. ophthalmicus profundus*,  
*cr.m.* crista mediana, *cr.sbnr.* crista subnarina, *cr.susp.* crista suspendens, *f.h.* fossa  
 hypophyseos, *fe.ench.* fenestra endochoanalis, *fe.npc.* fenestra nasalis posterior com-  
 munis, *fe.exp.* fenestra exonarina posterior, *fo.aup.* fossa autopalatina, *fo.nt.* pit for  
 anterior end of notochord, *la.pal.* palatal lamina of the fronto-ethmoidal shield, *o.vca.*  
 opening for *v. cerebialis anterior*, *pr.ling.* tongue-shaped process, *pr.bp.* processus  
 basipterygoideus, *Psph.* parasphenoideum, *sulc. aci.* groove for *a. carotis interna*,  
*sulc.apse.* groove for *a. pseudobranchialis efferens*, *sulc.marg.* sulcus marginalis.

## Pl. III

Specimen no. 3: *A* ethmoidal region in posterior view, *B* the same after removal of the  
 left nasal cavity cast, *C* latex cast in ventral view;  $\times 1.5$

*c.olf.* canalis olfactorius, *c.pap.* canalis paraapicalis, *c<sub>v</sub>n-b?* canal probably correspon-  
 ding to the ventral ramification of the canalis naso-basis in *Eusthenopteron*, *c.pap.*  
 canalis paraapicalis, *c.pr.* canal for *N. ophthalmicus profundus*, *cav.nas.* cavum nasale,  
*fov<sub>d</sub>m.* medial depression, *ioc.* infraorbital sensory canal.

## Pl. IV

Latex cast of the specimen no. 4: *A* in ventral view, *B* in posterior view;  $\times 1.5$

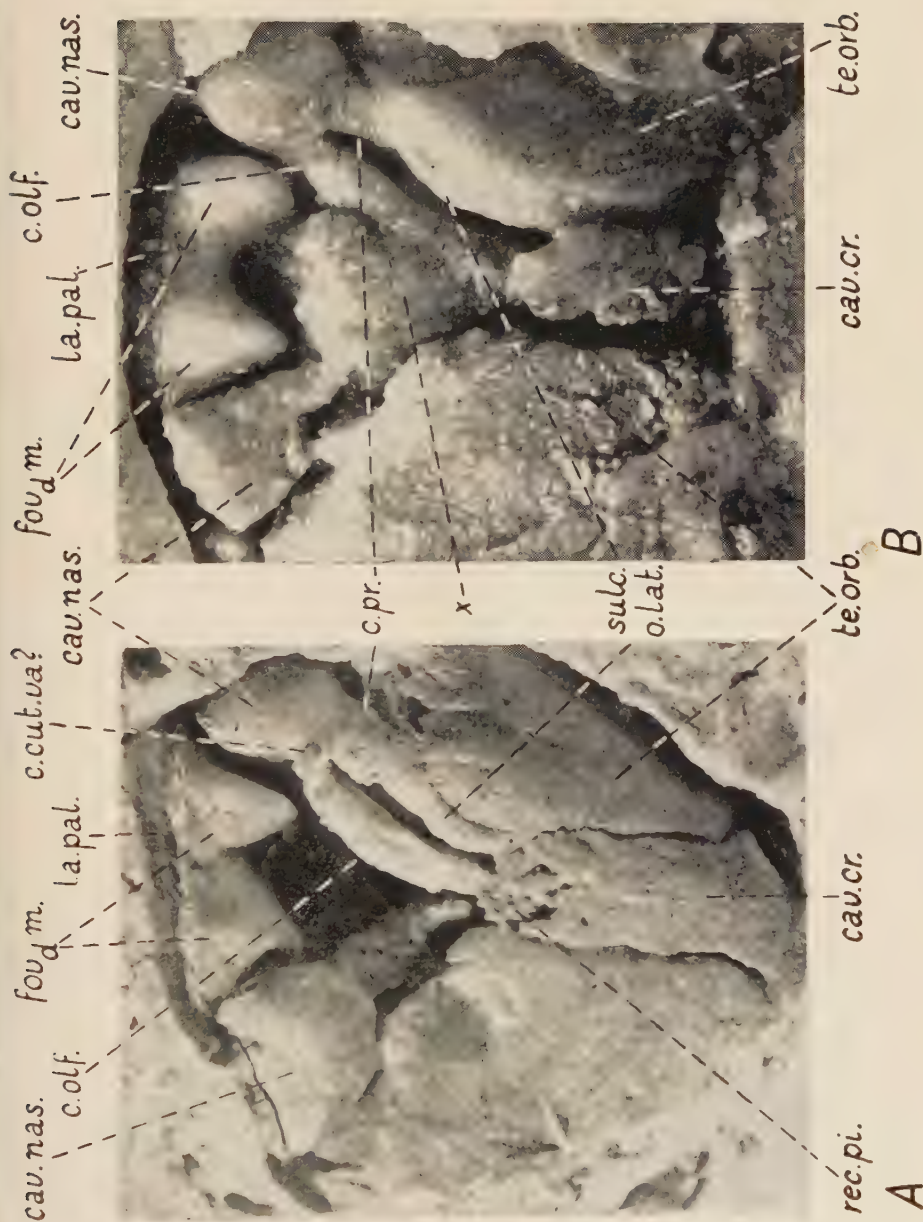
*c.in.trans.* canalis internasalis transversus, *c.o.lat* canal for *N. ophthalmicus lateralis*,  
*c.olf.* canalis olfactorius, *c.pr.* canal for *N. ophthalmicus profundus*, *cr.m.* crista me-  
 dian, *cr.sbnr.* crista subnarina, *d* denticle, *fe.ena.* fenestra endonarina anterior,  
*for.nutr.* foramina nutritii, *fov<sub>d</sub>m.* medial depression, *la.pal.* palatal lamina of the  
 fronto-ethmoidal shield, *pr.im.?* processus intermedius? *sulc.ln.* sulcus lateralis narium  
 and their branches.

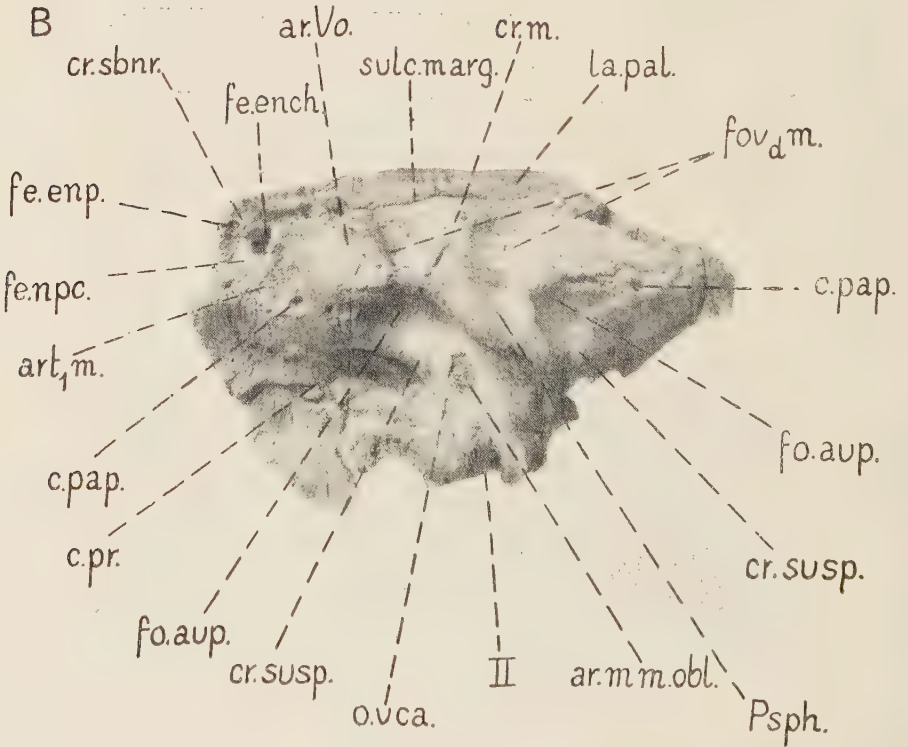
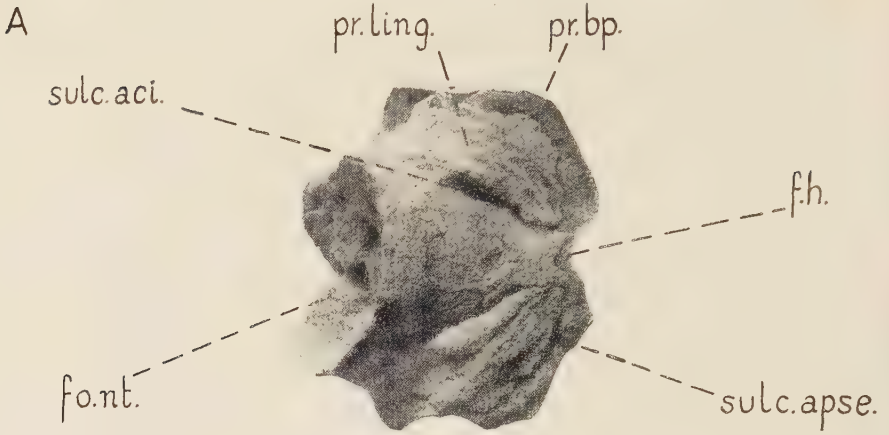
## Pl. V

Lower jaws: *A* specimen no. 7,  $\times 0.5$ ; *B* specimen no 8,  $\times 1.5$ ; *B'* latex cast of same;  
*C, D* latex casts of specimens no. 9 and 10,  $\times 1.5$ .

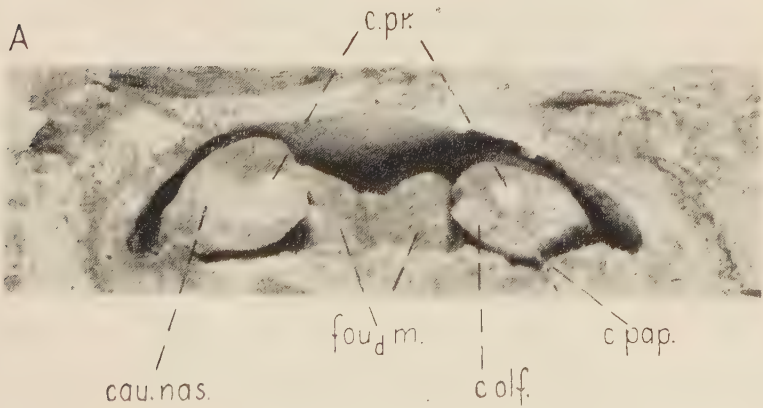
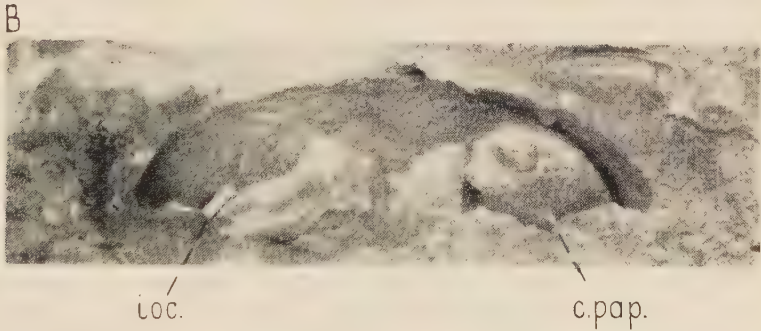
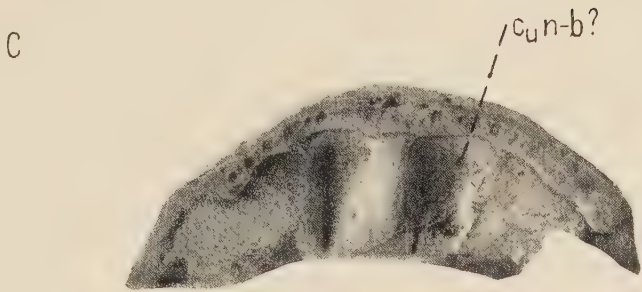
## Pl. VI

Latex casts of scales (fig. 1-15), teeth (fig. 18-23) and two undetermined bone fragments  
 (fig. 16, 17) of *Porolepis*; nat.size.

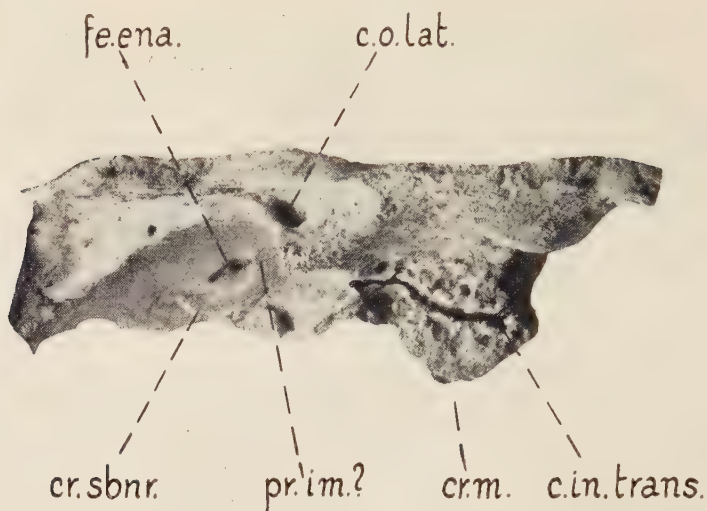




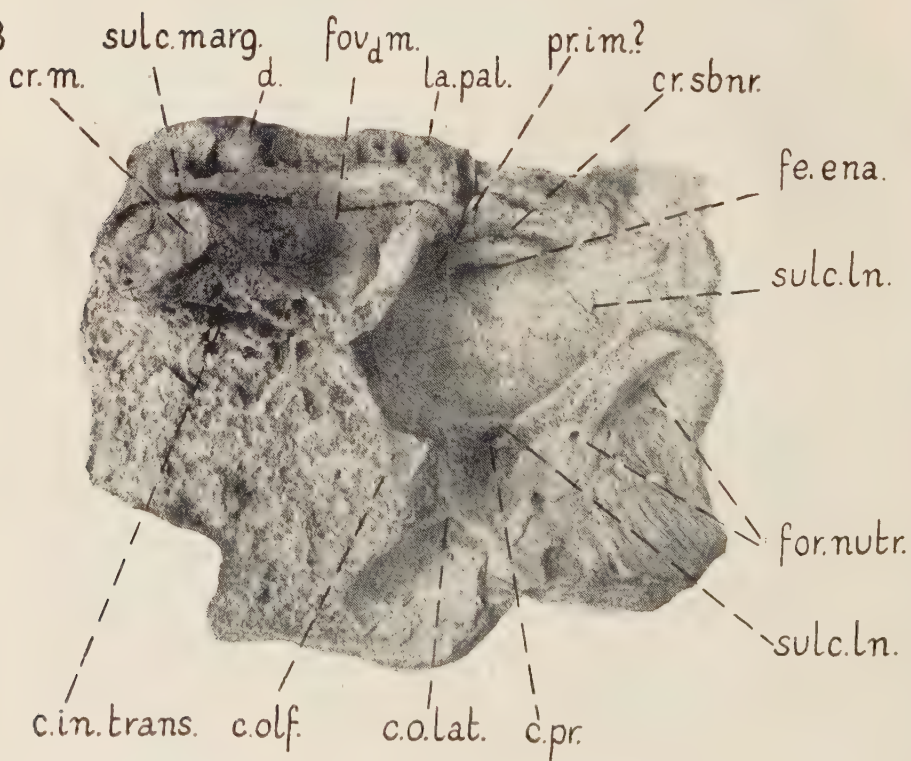




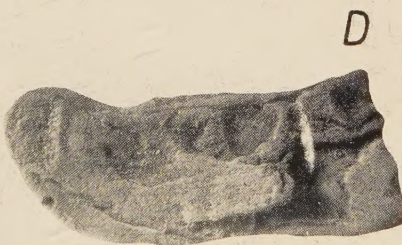
A



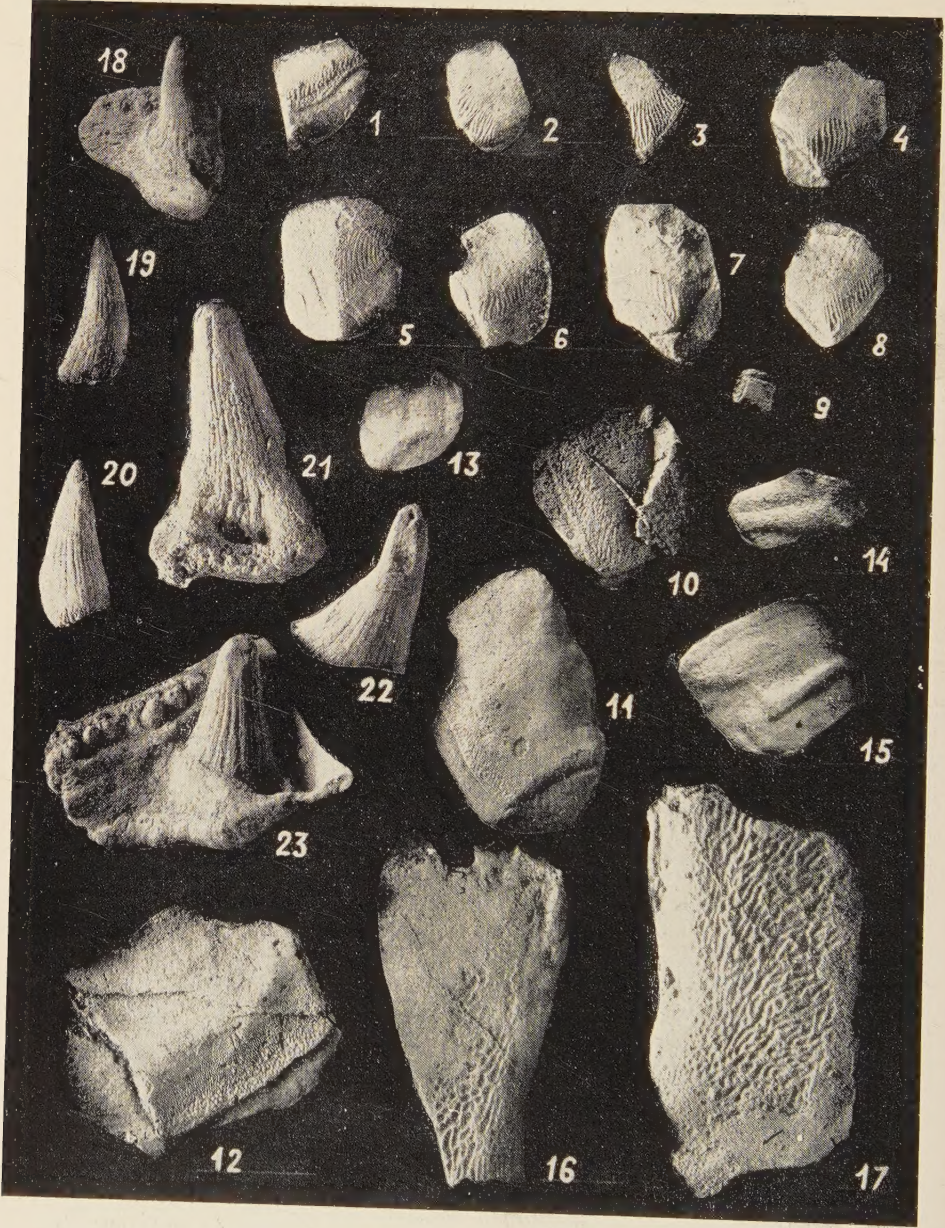
B

















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